DISSERTATION

SPATIAL ECOLOGY AND CONSERVATION OF TIGERS AND THEIR PREY IN THE CENTRAL TERAI LANDSCAPE, INDIA

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ABSTRACT

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Remnant populations of the world's ~3800 wild tigers (*Panthera tigris*) are generally small (< 20 adult individuals), subject to high rates of poaching, and confined to fragmented habitats with high levels of human disturbance. The species persistence requires an in-depth understanding of the suite of exogenous and endogenous factors that drive spatial heterogeneity in its occurrence and abundance. We intensively sampled tiger habitats in the populous 4500 km^2 Central Terai Landscape along the India-Nepal border and investigated the following questions: (a) what is the relative influence of protection designation (protected area or multiple use forests), prey availability, patch connectivity, human presence and habitat quality on landscape and local-scale tiger occurrence; (b) how do these and other factors drive spatial heterogeneity in tiger density at broad and fine spatial scales; and (c) what are the relationships between landscape fragmentation, adult sex ratios, and inter-specific interactions? We found that tiger occupancy and abundance were similar or higher in multiple use forests with high human use, than in several protected areas. Further, the distribution and abundance of prey and key habitats such as tall grasslands, –rather than protection designation, were the best predictors of spatial heterogeneity in tiger occupancy and density. The co-occurrence of tigers and humans in areas with high human use may be facilitated by refugia habitats such as tall grasslands and temporal partitioning of use. Habitat connectivity promoted high occupancy only when all habitats connected by corridors were effectively protected. Finally, we documented exacerbated potential for inter- and intra-sex competition and reduced population fitness in small, isolated

tiger populations with male-biased adult sex ratios. Overall, our study reveals that the establishment of protected areas alone may be an inadequate strategy to secure the future of wild tigers. We identified key ecological and anthropogenic factors that cumulatively enable the species persistence in populous human dominated landscapes.

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DEDICATION

For my parents and brother, eternal pilgrims on ageless paths

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INTRODUCTION

Protected areas (PAs) worldwide provide habitat and resources for imperiled species and help maintain intact ecological systems. However, PAs vary in the extent to which they support viable populations of imperiled species (Hokestra et al. 2005). Many PAs are too small for highly mobile mammals whose persistence requires additional resources from areas beyond extant PA boundaries (Smith et al. 1998). To maintain ecologically effective population sizes (Soule et al. 2003), many large carnivores will need to be conserved in habitats that experience varying degrees of human-use (Chapron et al. 2014). Meeting the conservation challenge posed by large carnivores requires knowledge of the potential for shared use of the landscape and an understanding of the ecological and social factors and incentives that promote carnivore occurrence in human dominated landscapes. Here, we focus on the former component— testing ecological hypotheses to explain spatial variation in tiger (*Panthera tigris*) occurrence at multiple spatial scales across a gradient of human disturbance, extending from PAs to multiple use forests (MUFs).

Our research was motivated by two primary considerations. First, while prioritizing tiger conservation in select and widely distributed PAs has been the foundational approach across the species range, this perspective largely ignores the contribution of the landscape matrix, including MUFs, and their significance for long-term tiger conservation. We believe this paradigm may be too narrowly focused because it does not acknowledge the local extinction of tigers from some PAs (Dinerstein et al. 2007), and the finding that some MUFs support tiger populations at higher

densities than nearby PAs (Jhala et al. 2011; Chanchani et al. 2014 a). Second, though recent studies have greatly increased our understanding of how prey occurrence, human disturbance and habitat connectivity influence tiger occurrence across landscapes (e. g. Karanth et al. 2011; Kanagaraj et al. 2011; Harihar & Pandav 2012; Barber-Meyer et al. 2013), significant knowledge gaps remain. In particular, previous studies have not fully investigated how the distribution of key habitat features, such as grasslands, influence tiger occurrence in PAs, MUFs or edge habitats.

The future of wild tiger populations is at a critical point and conservation strategies implemented over the next decade may well determine the fate of the species in Asia and elsewhere. Recently, multiple nations with wild tiger populations have jointly set a goal to double the world's tiger population by 2022 (The World Bank 2011). To further this conservation goal, our study addressed several important conservation questions including: 1) how does degree of protection (PAs or MUFs), and varying constraints on human-use, influence tiger occurrence at local and landscape scales; and 2) what resources (e.g., prey, habitat, etc.) and management practices promote tiger occurrence in MUFs with high levels of human-use?

To address these questions, we conducted tiger occupancy surveys in a 5400 km^2 area in the Central Terai Landscape (CTL) of north India. Abutting the international border between India and Nepal, the CTL is characterized by tall grasslands, swamps, and deciduous forests and high human population densities. The CTL consists of steep environmental gradients including: a human disturbance gradient extending from 'inviolate' PAs to MUFs with extensive resource extraction; a habitat quality gradient ranging from high quality grasslands and wetlands to sal (*Shorea robusta*) forests with low understory productivity and few palatable plant species; pronounced spatial variation in prey density and occurrence; variable patterns of isolation and

connectivity across habitat patches; and varying levels of wildlife management and protection from poaching.

Our study area in the CTL contained six large habitat patches (size range from 170 km^2 to 1050 km^2; Fig. 1), separated by farmlands and human settlements in India. We defined a patch as a homogeneous area of habitat (e.g., forest and grassland land cover) distinct from its surroundings where tiger movement is unlikely to be constrained by human land use (Johnsingh et al. 2004; Wikramanayake et al. 2004; Kanagaraj et al. 2013). Four of these patches were connected with other tiger habitats (PAs or MUFs) in Nepal (Johnsingh et al. 2004), but management practices within PAs and MUFs vary between the two countries. In Nepal, tigers and prey are relatively secure within PAs but are highly vulnerable to poaching in MUFs (Paudel 2012; Barber-Meyer et al. 2013; Chanchani et al. 2014 b). In contrast, in the Indian CTL, wildlife may indirectly receive similar "protections" in both PAs and MUFs because logging operations are widely dispersed and may lead to de-facto deterrents to poaching in the forest interior (Chanchani et al. 2014 a). In this context, we hypothesize that while PAs and MUFs may have similar tiger occupancy in the CTL, habitat patches connected with PAs in Nepal are expected to support higher rates of tiger occupancy than those connected with MUFs in Nepal. Additionally, we expect the relationship between tiger occurrence and human disturbance to be complex with human-disturbance thresholds beyond which tiger occupancy drops sharply. Finally, we hypothesize that high tiger occupancy can be achieved in areas of high human-use (MUFs), provided that these areas also support high prey densities and contain habitats (e.g., grasslands, wetlands) that provide essential cover and refugia from human disturbance.

METHODS

Study Area

The CTL straddles the states of Uttarakhand and Uttar Pradesh in north India (Fig. 1). Within this landscape our surveys were carried out in four PAs (Dudhwa National Park, Kishanpur, Katerniaghat, and Suhelwa Wildlife Sanctuaries) and in seven Reserve Forests (MUFs) including Pilibhit, Nandhour (Haldwani-Champawat-Terai East), and South Kheri (Nandhour and Pilibhit were granted Protected Area status in 2013 and 2014, respectively). About 40% of the CTL lies in the sub-Himalayan Bhabbar zone with the remaining area located along the Sharda and Ghagara River flood plains. Since about 1870 the CTL has experienced extensive timber harvest with extraction focused on sal (*Shorea robusta*) trees. Between 1870 and 1970 large parts of the landscape were intensively logged and tall-grass and wetland habitats were brought under cultivation. Today, fragmented habitat patches support small populations of tigers, elephants (*Elephas maximus*), swamp deer (*Rucervus duvaucelii*), rhinos (*Rhinoceros unicornis*), hog deer (*Hyelaphus porcinus*), and other endangered species. In India, over 3.3 million people currently live in approximately 3000 villages located less than five kilometers from the edge of the CTL forests.

Occupancy Estimation

Occupancy methods allow rapid, cost effective monitoring of species at large spatial scales and over multiple time periods (MacKenzie et al. 2006; Noon et al. 2012). For tigers and other species that frequently travel along trails and primitive roads, the requirement for replicate surveys can be achieved by assigning detection/non-detection outcomes to successive trail segments (Hines et al. 2010). This unique survey design is hierarchical: a ‘grid cell’ represents

the highest level sample unit and typically reflects the spatial ecology of the focal species; for example, the median home range size of a male tiger. Within each cell, survey transects or trails are separated into spatial subunits (segments) of a designated length. Occupancy models developed for hierarchical sampling designs typically estimate four parameters. Occupancy (Ψ), defined as the probability that a cell (site) is occupied by the focal species, is the primary parameter of interest. Given a cell is occupied, two additional parameters relate to species habitat use at finer spatial scales and account for spatial dependencies: θ' and θ are the probability that a segment is used given that the previous segment was or was not used, respectively. Finally, given that a segment is used, *p* is probability of detecting the species (tiger sign in this study). Spatial variation in any of the parameters can be modeled as a function of measured covariates via a logit link function (Hines et al. 2010). We employed a modified version of this model to include replication at the segment scale using two independent teams of observers, effectively doubling survey effort in each cell. This modification allowed us to utilize replicate surveys at each segment (via independent observers) to disentangle factors that influence fine scale habitat use (θ and θ'), from those that influence detection probability, akin to a multi-scale model (e.g., Nichols et al. 2007). For this reason, variation in fine-scale habitat use may be interpreted as an index of the frequency (or proportion) of habitat use within occupied cells (see Appendix 1.1). Our survey design also yields more precise parameter estimates by increasing the cumulative detection probability (p^*).

Field Sampling

We mapped forest and grassland areas within 60, 166 km^2 cells, constituting all primary tiger habitats within the CTL; 34 of these cells were wholly or partially located in PAs. Cell size was selected to reflect the typical home range of adult male tigers (Harihar & Pandav 2012).

Survey effort in each cell was proportional to the amount of suitable habitat—for example, in a cell with 100% habitat, 40 km of trails were independently surveyed by both teams. Within each cell, trails were selected so that forest and grassland habitats were sampled in proportion to their prevalence in the cell. To representatively sample anthropogenic disturbance, selected trails intersected both edge and interior habitats. Because several ungulate species show strong affinities for specific habitat types (Dinerstein 1980), and may be excluded from areas with high levels of human disturbance (Madhusudan 2004), we believe that sampling across habitat and disturbance gradients (within and among cells) allowed us to also sample across a prey abundance gradient.

Within each cell, surveys were conducted by pairs of observers (teams) walking designated trails looking for evidence of tigers, prey, and livestock (e.g., scat, tracks, and direct sightings). Surveys were conducted between October 2010 and November 2012, but each cell was surveyed within a 5 day period to minimize violations of the closure assumption for occupancy estimation (Karanth et al. 2011). Two teams surveyed selected trails and independently recorded several covariates for each 250m length of trail. Covariates included the number of detected tracks and other signs for tigers and each of seven focal prey species, the number of humans and livestock seen, and the presence of water bodies, dwellings, farmland, and grass in the forest understory in the immediate vicinity of the trails. To account for potential variation in detection probability, we scored the ability of the soil substrate to record sign by ranking our own footprints' visibility at 50 meter intervals along each trail segment. In addition, we ranked the intensity of bicycle, automobile treads and cattle tracks which could obscure wildlife signs (Table 1.1).

Covariates and Hypotheses

We used the above data to derive eight field covariates to evaluate environmental factors possibly affecting detection probability (*p*), fine scale habitat use (θ and θ') and occupancy (Ψ) (Table 1.1). We summarized covariate data collected from adjacent 250 m trail lengths to a 1 km segment scale (Table 1.1). We hypothesized that our ability to detect tiger signs along used trail segments would be affected by soil substratum conditions and intensity of vehicle and livestock use.

Because tiger occurrence is influenced by prey abundance (Karanth et al. 2011), we derived two covariates that described the proportion of sampled habitat, with sparse or multiple prey signs. Specifically, for each cell *i* , we calculated: $PreyER_i = \sum_{s=1}^{7} prop_s$ and $PreyHigh_i = \sum_{s=1}^{7} proph_s$, where $prop_s$ is the proportion of 250 m trail lengths in cell *i* on which sign of prey species *s* was detected and $proph_s$ is the proportion of trail lengths in cell *i* with high abundance (multiple sets of tracks) for prey species *s*. The proportions for all seven ungulate species were summed to obtain the two covariates we hypothesized would positively affect tiger occurrence at both broad and fine spatial scales (Table 1.1). Hypothesizing that tiger occupancy at both spatial scales would decline in areas of high human disturbance, we calculated a human-livestock encounter rate for each cell, defined as the total number of humans and livestock encountered per kilometer during surveys. Further, we predicted that estimates of fine scale habitat use (θ and θ') would be lower in segments bordered by human dwellings and agriculture and higher in segments adjacent to water bodies and forests associated with grassy understory.

We also computed eight covariates from remotely sensed data to address biological hypothesis related to tiger occurrence. We hypothesized that the extent of protected area (PA) or

multiple use forests (MUF) within a cell may relate to tiger occurrence. Importantly, we expected that tiger occupancy and fine scale habitat use would be most influenced by other habitat attributes such as total habitat area (PA + MUF area in cell) or the extent of grasslands. Further, we hypothesized that occupancy would reflect a cell's degree of isolation and, for cells adjacent to the international border, the degree of protection in neighboring patches in Nepal. We expected tiger occupancy would be highest for cells in patches connected with PAs in Nepal, next highest in isolated patches, and lowest in patches connected with MUFs in Nepal. Finally, we hypothesized that stream length, distance from the Nepal border (a zone of high human disturbance) and less edge habitat in a cell would positively influence tiger occupancy. We tested for collinearity among covariates and retained covariates with correlations (r) <0.5. The covariate stream length was omitted from our analyses because it was highly correlated with grassland area (Grass), $r = 0.58$.

Collectively, our set of covariates allowed us to test five broad hypotheses related to spatial variation in patterns of tiger occupancy—specifically, tiger occurrence is affected by: 1) habitat (described by the covariates PA, MUF, TotalArea and Grass); 2) prey occurrence or relative abundance (PreyER and PreyHigh); 3) connectivity status (Conn); 4) human and livestock presence (HumLive); and 5) proximity to habitat edges (EdgeLen and NepalDist). Considered individually, we expected support for these hypotheses to be ordinally ranked as: prey and habitat > connectivity > proximity to edges > human and livestock presence. Since tiger occupancy may be best explained by multiple hypotheses, we fit models that combined covariates from each of the five categories, in addition to models representing a single hypothesis. We were especially interested in testing our prediction that habitat and prey covariates would strongly influence tiger occurrence across broad habitat connectivity,

disturbance and other environmental gradients. A subset of the aforementioned covariates was also used to test hypotheses about fine scale habitat use by tigers (Table 1).

Analysis

We fit detection data to occupancy models using program MARK (White & Burnham 1999) and ranked models using AIC_c (Burnham & Anderson 2002). Due to the potentially large number of models, we employed a step-wise process to model building and evaluation. First, we identified 64 alternative global models from our *a priori* model set, all with the following structure:

Ψ (HumLive + *habitat* + *prey* + HumLive * *habitat*), θ & θ' (Understory + H_20 + D-Ag +*habitat* + *prey* +HumLive), *p* (Soil + Tread). Given uncertainty about the 'optimal' combination of *habitat* and *prey* covariates, we considered all possible combinations of a single *habitat* covariate (TotalArea, Grass, PA or MUF) and a single prey covariate (PreyHigh or PreyER) (Appendix 1.2). This modeling step enabled us to assess the relative importance of PA and MUF habitat area, total habitat area (TotalArea) and grassland area on tiger occurrence. Of these covariates, only those that appeared in highly supported models were carried forward into subsequent modeling steps.

In step two we used the best supported global model structure(s) to test hypotheses relating detection probability (*p*) to variation in soil substrate and intensity of vehicle and livestock use (Appendix 1.3). We selected the model with lowest AIC_c score, and retained this detection probability structure in all subsequent models.

Next, we evaluated the influence of segment-scale attributes such as water bodies, human development (human dwellings and agriculture), grassy understory, and cell-scale attributes such as prey relative abundance, extent of grasslands and human and livestock encounter rates on fine

scale tiger habitat use (θ and θ') (Appendix 1.4). Again, we selected the model with lowest AICc score and retained this structure on θ and θ' in all subsequent models. Finally, we tested 23 *a-priori* models to ascertain how connectivity, human disturbance and proximity to edge covariates—singly or in additive or interactive combinations with habitat and prey—influenced tiger occupancy (Table 1.2).

For mapping purposes, cell specific occupancy estimates were derived using the logit transformation and estimated regression coefficients from the best supported model. Because our sampling was a complete survey of all forest and grassland habitats in the Indian CTL, we were able to estimate overall the tiger occupancy in the CTL as: $\widehat{\Psi} = \sum_{i=1}^{60} a_i \Psi_i$, where a_i is the proportion of total habitat area in cell *i* (Karanth et al. 2011). We used the delta method to compute the standard error of $\widehat{\Psi}$.

RESULTS

Collectively, the two teams surveyed 2018 km of trails. Tiger signs were encountered within 42 of the 60 166 km^2 cells, and on 336 of the 1009 one kilometer trail segments. The naïve occupancy estimate for tigers was 0.70. Of the 18 cells where no tiger signs were detected, 13 were located wholly or partially in PAs previously occupied by tigers (Jhala et al. 2011; Johnsingh et al. 2004). We detected a single tiger sign in Suhelwa Wildlife Sanctuary, a PA which historically supported a large tiger population, and no tiger signs in large areas of the Dudhwa and Katerniaghat PAs. Unexpectedly, tiger occupancy was high in some MUFs within the CTL, with the exception of Nandhour Reserve Forest (Fig., 1.1). From our best supported occupancy model (described below), the estimated proportion of the CTL occupied by tigers was

0.72 (SE 0.020). We note that the reported standard error may be biased low -- because occupancy in habitat patches connected with PA's in Nepal (represented by PA-Conn, which features in the top occupancy model) -- was estimated near a boundary value (~1).

Influence of PA, MUF, Grassland and Total Habitat Area on Tiger Occupancy and Fine Scale Habitat Use

Among the 64 alternative global models, the best supported models included grassland habitat (Grass) and the *prey* covariates (PreyHigh and PreyER, Appendix 1.2). The covariates PA, MUF, and TotalArea were not in the top models, suggesting that habitat quality rather than total habitat area or protection status best explained variation in tiger occupancy within the CTL (Appendix 1.2). The two best supported global models differed in the inclusion of the *prey* covariate, PreyHigh or PreyER, for fine scale habitat use, ψ(PreyHigh + Grass + HumLive + Grass*HumLive), θ and θ'(H_2O + Grass + *prey* + HumLive), p(Soil + Tread). These model structures were used in subsequent analysis steps.

Covariate influence on tiger detection probability (p), fine scale habitat use (θ and θ') and occupancy (ψ)

The top detection probability structure included the covariates Soil and Tread (vehicle/ cattle signs) and had 41% of the overall AIC_c weight (*w*), nearly two times more support than the next best model. This detection structure had high support, regardless of the *prey* covariate used to model fine scale habitat use (Appendix 1.3). Consistent with our predictions, disturbed soil substrate and high levels of vehicle and livestock use decreased *p*. For the best model, detection probability estimates ranged from 0.73 (SE 0.03) for used segments with 'poor' soil and high

disturbance to 0.89 (SE 0.03) for used segments with 'good' soil and few vehicle and cattle tracks.

Collectively the top four fine scale habitat use models revealed that Grass, PreyER, HumLive and H2O (prevalence of water bodies along segments) were the most important covariates influencing fine scale tiger use in occupied cells (Table 1.2; Fig., 1.2). Consistent with our predictions, the covariate HumLive negatively influenced tiger use while the three other covariates (Grass, PreyER and H2O) had positive coefficient values (Table 1.2). From the top model, estimates of use were approximately twice as high for θ' (0.63, SE=0.04) than θ (0.31, SE=0.03), for segments with the maximum value of water bodies (H2O = 4) and the other covariates at their mean values (Fig., 1.2a-d). The estimates emphasize the strong correlated nature of trail sampling methods. The other segment-scale covariates (D-Ag, Understory) were not well supported; though these covariates appeared among the top five models they were considered uninformative (see Burnham and Anderson 2002 and Arnold 2010 for a discussion of uninformative parameters).

Tiger occupancy (ψ) was influenced by an additive combination of high prey encounter rate and connectivity; a model with these covariates had far better support than the global model structure (Table 1.3, Appendix 1.5). From the best supported occupancy model, Ψ(PreyHigh+ Conn, *w*=0.71), While habitat patches in the CTL connected by corridors to PAs in Nepal had high tiger occupancy, patches that were either connected with MUFs in Nepal, or isolated, had lower occupancy, especially for cells where prey signs were sparse. (Fig., 1.3). The covariate Grass was included in three of the models with support (Table 1.3), but this covariate was largely uninformative, with little influence on tiger occupancy (Arnold 2010). Similarly, minimal or no support for the covariates HumLive, EdgeLen, and NepalDist suggest that human-disturbance

may have minimal influence on occupancy if habitat and prey resources are available, and 'effective' protection is exists. However, the coefficients signs on these covariates were consistent with our a priori predictions (Tables 1.1 and Appendix 1.5).

DISCUSSION

Current tiger conservation strategies emphasize the importance of protected areas where human-uses such as timber harvest are prohibited or severely constrained. In India, strategies to expand conservation efforts to include management for tiger and their prey in working (human-dominated) landscapes have not been part of a comprehensive conservation portfolio. Our study specifically focused on documenting the occurrence and environmental relationships of tigers in a human-dominated, trans-boundary landscape. Unexpectedly, we recorded similar probabilities of tiger occupancy in PAs and MUFs that were subject to timber harvest and extensive day time use by humans and livestock. Some MUFs had extensive areas of suitable wildlife habitats, supported tiger and prey populations with densities nearly twice as high as some PAs in the CTL (Chanchani et al. 2014 a). We found lower estimates of tiger occupancy in some PAs (e.g. Suhelwa Wildlife Sanctuary) that historically supported large tiger populations (Singh 1993). Our results do not undermine the overall importance of PAs for tiger conservation, but instead suggest that low tiger occurrence in some PAs may reflect systemic failures of management and law enforcement, and ultimately inadequate financial support for conservation.

Overall, the most important factors influencing tiger occupancy were the availability of prey (PreyHigh) and connectivity (Conn) among habitat patches. Importantly, we found that conditions favoring high levels of occupancy are not restricted to PAs but can occur in some

MUFs. Because the degree of human-use, management practices and protection varies throughout the CTL, however, the relationship of tiger occupancy to prey availability and habitat connectivity (Conn) can be complex. Maintaining multiple large patches of habitat connected by a system of corridors, for example, will not guarantee high levels of tiger occupancy unless these area are effectively protected from poaching, and prey are abundant (Fig.,1.3).

Our results suggest that relatively high abundance of prey and grassland habitats support tiger habitat use and occupancy at different spatial scales independent of designated protection status. Prey encounter rates (PreyHigh or PreyER) positively influenced tiger occupancy and fine scale habitat use within occupied cells (Fig.,1. 3 and 2a). In contrast, grassland area only influenced the local distribution of tigers within occupied cells (Fig., 1.2 b). We hypothesize that retaining undisturbed wetland and tall-grass habitats within MUFs may provide a spatio-temporal refugia for tigers and humans to achieve co-occurrence (Harihar et al., 2013). Preliminary evidence for temporal segregation between humans and tigers comes from our camera trap surveys in sections of this landscape, where four times more day-time photo-captures of tigers were recorded in PAs than MUFs (Appendix 1.6).

We did not directly assess spatial correlation in tiger occurrence. Concentrated areas of high occupancy could arise from three processes: spatial contagion of critical resources, favorable management practices at the scale of a habitat patch, and an increased likelihood of colonization following a local extinction event. One consequence may have been to overestimate the role of landscape connectivity—covariate metric Conn—as the strongest predictor of tiger occupancy. Finally, we note that high occupancy estimates in our study area may not reflect high tiger abundance. To effectively monitor changes in the status of small populations of animals, it

is important to also estimate density, abundance and other state variables from individual based capture-recapture analyses.

Conservation and Policy Implications

Our findings support the argument that tiger conservation strategies should adopt a landscape perspective, inclusive of PAs and MUFs (Wikramanayake et al. 2011), rather than a narrow focus on PA's (Waltson et al. 2010). The current tiger conservation paradigm in India emphasizes the importance of PAs that preclude human-use. However, our results from the CTL suggest that some degree of shared space-use between humans and tigers is possible. We are not assuming behavioral "co-existence" as done by other researchers (Carter et al. 2012). Instead, we propose that MUFs that restrict human access to daytime hours, and have daytime refugia for tigers, effectively expand the amount of suitable tiger habitat beyond that found in PAs. While co-occurrence may be achieved by a temporal partitioning of space, areas of high overlap between tigers and humans increase the likelihood of human-tiger conflict (Chanchani et al. 2014a), and at the fine scale, tigers seemed to avoid using areas of high human-livestock use. Given our belief that long-term tiger conservation will benefit from measures that promote the species occupancy in working landscapes, we are currently investigating potential thresholds of human-use beyond which tigers and human co-occurrence is not possible. We recognize that the current distribution of tigers in the CTL is likely not at equilibrium with environmental conditions and resources (particularly prey abundance), which may vary over space and time. Thus, we recommend a continuation of occupancy surveys in order to estimate cell-scale colonization and extinction rates and the covariates related to variation in these rates (Yackulic et al. 2015).

The distribution of tigers in the CTL suggests that the current classification of conservation areas into source-populations, PAs, MUFs, core, and buffer zones are not necessarily reliable predictors of tiger distribution at the landscape scale. In the CTL, some of the most productive tiger habitats are located in poorly protected riparian areas and in buffer zones heavily grazed by cattle (Chanchani et al. 2014 b). As a result of current levels of human-use and the fragmented nature of the landscape, tigers in the CTL may have a metapopulation structure. Metapopulation equilibrium requires a balance between extinction/colonization dynamics and emphasizes the importance of existing corridors that span the India-Nepal border. These areas provide essential connectivity between habitat patches and allow for recolonization of suitable habitat areas following local extirpation. We recommend that existing corridors be enhanced and patrolled by law enforcement to minimize poaching. The restoration of key corridors, including Basanta, Laljhari, Shuklaphanta-Pilibhit, Gola and Boom-Bharmadev (Fig., 1.1) for example, should be a conservation priority for the Governments of India and Nepal before opportunities for their protection are precluded.

To prevent declines in tiger occupancy, more effective anti-poaching patrolling and law enforcement are required, both in PAs and in MUFs across the landscape. Specifically, more rigorous anti-poaching measures to recover tiger and prey populations are needed in MUFs in Nepal. Although several MUFs in Nepal have been successfully afforested (Nagendra 2007), measures to protect wildlife in these areas are generally inadequate (Smith et al. 1998; Wegge et al. 2009) and expanding human settlements in several MUFs pose a significant conservation challenge (Chanchani et al. 2014 b). Nepal's army, in contrast, scrupulously protects its PAs. In India, the situation is different: several PAs and MUFs have experienced recent declines in tiger populations (e.g., Suhelwa, Dudhwa, Nandhour), and there is an urgent need to overhaul

protection strategies both in PAs and MUFs, while also building community support for conservation through sustainable development initiatives. Special conservation efforts also need to be focused along India's international border with Nepal, a zone of both low tiger occupancy and prey abundance. Finally, in order to sustain tiger populations in working landscapes, we recommend that critical wildlife habitats that can serve as essential refugia and corridors be identified within MUFs, and delineated as priority conservation areas. The demarcation and stringent protection of critical wildlife habitats in working landscapes is an essential component of a comprehensive conservation strategy for tigers in South Asia.

TABLES

Table 1.1. Details of field survey (FS) and remotely sensed (RS) covariates and their expected influence (direction and strength) on parameters of interest: cell scale occupancy (Ψ), fine scale habitat use (θ and θ′), and detection probability (*p*). The relationship between the parameter of interest and the covariate is assumed to be linear (on the logit scale) unless specified otherwise.

Data Source	Covariate name and abbreviation	Covariate description	Observed range of values	Parameter and expected influence
FS	Prey Encounter Rate (PreyER)	Sum of the proportion of 250 m lengths of trail within a cell where ungulate prey was encountered, for the following seven species: chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), hog deer (*Hyelaphus porcinus*), wild pig (*Sus scrofa*), swamp deer (*Rucervus duvaucelii*) and goral (*Nemorhaedus griseus*)	0.2 - 3.3	Ψ (+) θ and θ' (+)
FS	High Prey Encounter Rate (PreyHigh)	Sum of the proportion of 250m trail lengths in a cell where signs of seven ungulates species were encountered at a 'high' intensity (multiple sets of tracks on a trail length)	0 - 1.4	Ψ (+ + +) θ and θ' (+++)
FS	Human & Livestock Encounter Rate (HumLive)	Encounter rate for humans and livestock (total count/ km of trail surveyed)	0 - 48 individuals/km	Ψ (-), θ and θ' (-) (linear or quadratic)

FS	Prevalence of water bodies (H_20)	The presence of water bodies, recorded as yes (1) or no (0) for each 250m length of trail; values were summed for each 1km segment	0 – 4	θ and θ' (+)
FS	Prevalence of Dwellings & Agriculture (D-Ag)	The presence of dwellings and agriculture, recorded as yes (1) or no (0) for each 250 m trail interval; values were summed for each 1km segment	0 – 8	θ and θ' (-)
FS	Prevalence of Grassy Understory (Understory)	The presence of grassy understory in forests, recorded as present (1) or not present (0) for each 250 m trail interval; values were summed for each 1km segment	0 – 4	θ and θ' (+)
FS	Number of 250m trail lengths with poor detection qualities (Soil)	A 250 m trail length was classified as 'poor substratum' (1) if ≥60% of the 50m intervals were categorized as 'poor visibility'; values were summed for each 1km segment	0 – 4	p (-)
FS	Intensity of vehicle/livestock use (Tread)	A 250 m trail length was classified as 'high tread' (1) if ≥ 50% of the 50m intervals contained automobile, bicycle or cattle treads/tracks; values were summed for each 1 km segment, across all three categories	0 – 12	p (-)
RS	Total Area (TotalArea)	Area (km^2) within each cell comprised of primary tiger habitats (amount of MUF + amount of PA)	18 – 165 km^2	Ψ (+) θ and θ' (+)
RS	Grassland Area	Area (km^2) within each cell comprised of grasslands (swampy	0 – 48 km^2	Ψ (++)

	(Grass)	tall grass and short grass)		θ and θ' (+ +)
RS	StreamLength	Length of streams and rivers and perimeter of water bodies within each cell (km)	0.25 – 69 km	Ψ (+ +)
RS	Habitat Edge Length (EdgeLen)	Length of habitat edge (km) with human land use in each cell; cells with greater overall edge length are expected to be more disturbed	12 – 180 km	Ψ (-)
RS	Distance to International Border (NepalDist)	Distance (km) from the centroid of a cell to the India - Nepal (international) border	0 – 55 km	Ψ (+)
RS	Amount of Protected Area (PA)	Extent of overall cell area that has PA status (km^2)	0 – 147 km^2	Ψ (+) θ and $\theta'(^+)$
RS	Amount of Multiple Use Forest (MUF)	Extent of overall cell area that has MUF status (km^2)	0-156 km^2	Ψ (-) θ and θ' (-)
Lit. review	Habitat Connectivity Index (Conn)	This covariate is categorical with three levels denoted as: PA-Conn = forest in India connected with non-PA in Nepal; MUF-Conn = forest in India connected with PA in Nepal; and No-Conn (reference) = isolated forest patch in India .	Indicators of each category (1 or 0)	Ψ (++) (PA-Conn> No-Conn >MUF-Conn)

Table 1.2. Model selection results for supported models of fine scale habitat use (θ and θ') in the CTL. Estimated coefficients (β) and standard errors are given for models with w>0.

Model[a,b]	Δ AIC[c]	w^d	K^e	$-2l^f$	Estimated β (SE)						
					D-Ag	H_2O	Understory	Grass	PreyER	PreyHigh	HumLive
θ&θ'' (H2O + Grass + PreyER + HumLive)	0.00	0.35	14	1601.38		0.14 (0.05)		0.03 (0.01)	0.43 (0.17)		-0.04 (0.01)
θ&θ' (D-Ag + H2O + Grass + PreyER + HumLive)	2.83	0.09	15	1600.64	-0.09 (0.10)	0.13 (0.05)		0.03 (0.01)	0.40 (0.17)		-0.03 (0.01)
θ&θ'(H2O + Grass + HumLive)	2.84	0.09	13	1607.64		0.12 (0.05)		0.03 (0.01)			-0.05 (0.01)
θ&θ' (H2O + Understory + Grass + PreyER + HumLive)	2.97	0.08	15	1600.77		0.13 (0.05)	0.04 (0.05)	0.03 (0.01)	0.41 (0.18)		-0.03 (0.01)
θ&θ' (H2O + Grass + PreyHigh + HumLive)	4.26	0.04	14	1605.64		0.11 (0.05)		0.03 (0.01)		0.32 (0.22)	-0.04 (0.01)
θ&θ' (Grass + PreyER + HumLive)	4.33	0.04	13	1609.13				0.03 (0.01)	0.37 (0.17)		-0.03 (0.01)
θ&θ' (D-Ag + H2O + Grass + HumLive)	4.45	0.04	14	1605.83	-0.13 (0.10)	0.11 (0.05)		0.03 (0.01)			-0.05 (0.01)
θ&θ' (H2O + Understory + Grass + HumLive)	4.66	0.03	14	1606.04		0.11 (0.05)	0.06 (0.05)	0.03 (0.01)			-0.05 (0.01)
θ&θ' (H2O + Grass + PreyER)	5.03	0.03	13	1609.83		0.11 (0.05)		0.02 (0.01)	0.70 (0.15)		
θ&θ' (Grass + HumLive)	5.78	0.02	12	1613.86				0.03 (0.01)			-0.05 (0.01)
θ&θ' (D-Ag + H2O + Understory + Grass + PreyER + HumLive)	6.02	0.02	16	1600.08	-0.09 (0.10)	0.13 (0.05)		0.03 (0.01)	0.38 (0.18)		-0.04 (0.01)

θ&θ' (Grass + PreyHigh + HumLive)	6.13	0.02	13	1610.93				0.03 (0.01)		0.38 (0.22)	-0.04 (0.01)
θ&θ' (D-Ag + Grass + PreyER + HumLive)	6.29	0.02	14	1607.67	-0.12 (0.10)			0.03 (0.01)	0.33 (01.7)		-0.03 (0.01)
θ&θ' (D-Ag + H2O + Grass + PreyHigh + HumLive)	6.36	0.01	15	1604.16	-0.12 (0.10)	0.11 (0.05)		0.03 (0.01)	0.29 (0.23)		-0.04 (0.01)
θ&θ' (D-Ag + Grass + HumLive)	6.48	0.01	13	1611.28	-0.16 (0.10)			0.03 (0.01)			-0.04 (0.01)
θ&θ' (Understory + Grass + PreyER + HumLive)	6.56	0.01	14	1607.94			0.05 (0.05)	0.02 (0.01)	0.34 (0.17)		-0.03 (0.01)
θ&θ' (D-Ag + H2O + Understory + Grass + HumLive)	6.67	0.01	15	1604.48	-0.12 (0.10)	0.12 (0.05)	0.05 (0.05)	0.03 (0.01)			-0.05 (0.01)
θ&θ' (H2O + Understory + Grass + PreyHigh + HumLive)	6.68	0.01	15	1604.48		0.11 (0.05)	0.05 (0.05)	0.03 (0.01)		0.28 (0.23)	-0.05 (0.01)

Footnotes

a: ψ and *p* structure for used for all models: ψ(PreyHigh + Grass + HumLive + Grass * HumLive) and *p* (soil + tread).

b: Covariates: D-Ag: prevalence of dwellings and agriculture along trail segments; H2O: prevalence of water bodies along trail segments; Understory: prevalence of grassy understory along trail segments; Grass: Grassland area in cell; PreyER: Sum of encounter rates for prey signs (7 species) along 1 km segments within a cell; PreyHigh: Sum of trail lengths with 'high' encounter rates for multiple prey signs (7 species) along 1 km trail segments within a cell; HumLive: Sum of human and cattle encounter rates along 1 km trail segments within a cell.

For detailed information for covariates, see Table 1.

c: ΔAIC_c is the difference in AIC_c between the best supported model and any given model.

d: *w* is the AIC_c model weight.

e: *K* is the number of parameters

f: -2*l* is twice the negative log likelihood.

Table 1.3. Model selection statistics, estimated coefficients and standard errors, for occupancy models ($\Sigma w = 1$) using data from tiger sign surveys in the CTL.

Model[a]	ΔAICc[b]	w^c	K[d]	$-2l^e$	Estimated β (SE) Conn-PA	Conn-MUF	PreyHigh	Grass	HumLive
Ψ(PreyHigh + Conn)	0.00	0.71	12	1601.98	19.84 (1784.43)	1.63(1.76)	10.15 (4.37)		
Ψ(PreyHigh + Grass + Conn)	2.13	0.25	13	1600.84	23.6 (2544.04)	5.35 (5.03)	10.87 (5.12)	0.41 (0.45)	
Ψ(PreyHigh + Grass)	7.49	0.02	11	1612.61			8.77 (4.15)	0.59 (0.43)	
Ψ(PreyHigh + Grass + HumLive)	9.03	0.01	12	1611.01			8.90 (4.83)	0.76 (0.37)	-0.13 (0.10)

Footnotes
a: Covariates: PreyHigh: High Prey Encounter Rate; Conn: categorical habitat connectivity covariate with three categories, Conn-PA indexes patches in the CTL connected with Nepal PAs, and Conn-MUF indexes patches in the CTL connected with MUFS in Nepal, and Non-conn indexes isolated patches(reference); Grass: grassland area; HumLive: human and livestock encounter rate. The model specification for the parameters θ, θ' and *p* was: θ&θ' (Grass + PreyER + HumLive + H2O), *p* (Soil + Tread). For complete list of occupancy models and coefficient estimates, see Appendix 1.5.
b: ΔAIC_c is the difference in AIC_c between the best supported model and any given model.
c: *w* is the AIC_c model weight.
d: *K* is the number of parameters
e: $-2l$ is twice the negative log likelihood

FIGURES

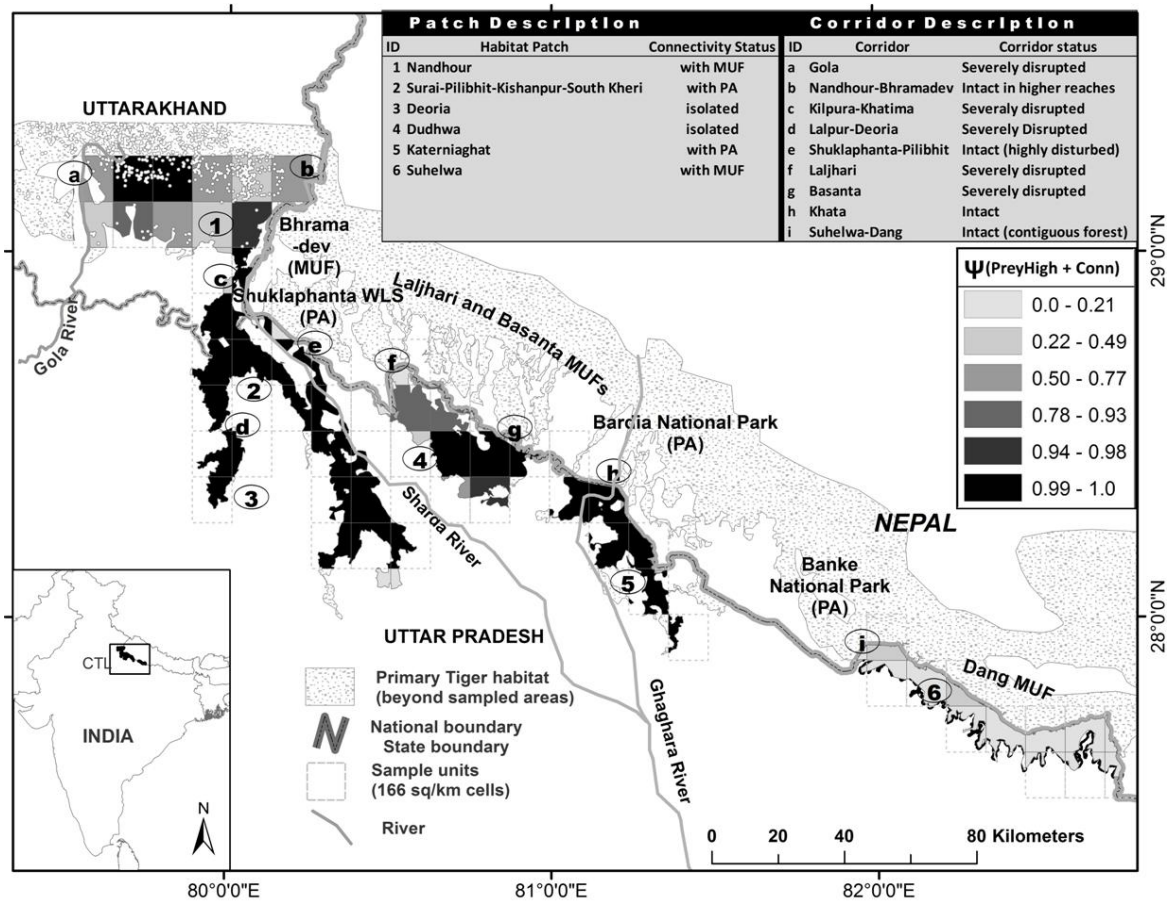

Figure 1.1. Map of the Central Terai Landscape delineating the boundaries of six habitat patches, adjacent protected areas (PA) and multiple use forests (MUF) in Nepal, key corridors and estimates of cell specific occupancy probabilities from the best supported model.

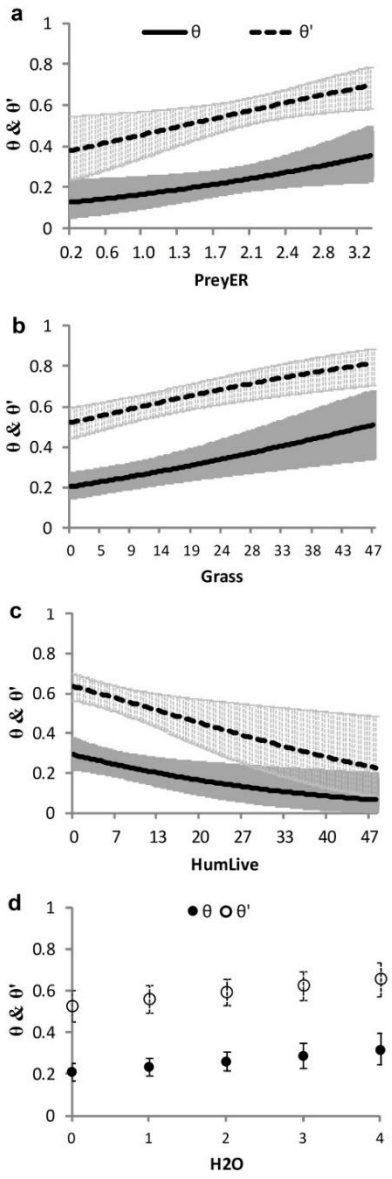

Figure 1.2. Relationship between fine scale habitat use (θ and θ') and prey relative abundance (a); grassland area (b); intensity of human and livestock use and(c); water along trail segments (d). All estimates are from the best supported model structure: θ&θ' (H2O + Grass + PreyER + HumLive). All covariates in the model, other than the ones plotted on the x axis, are at their mean values.

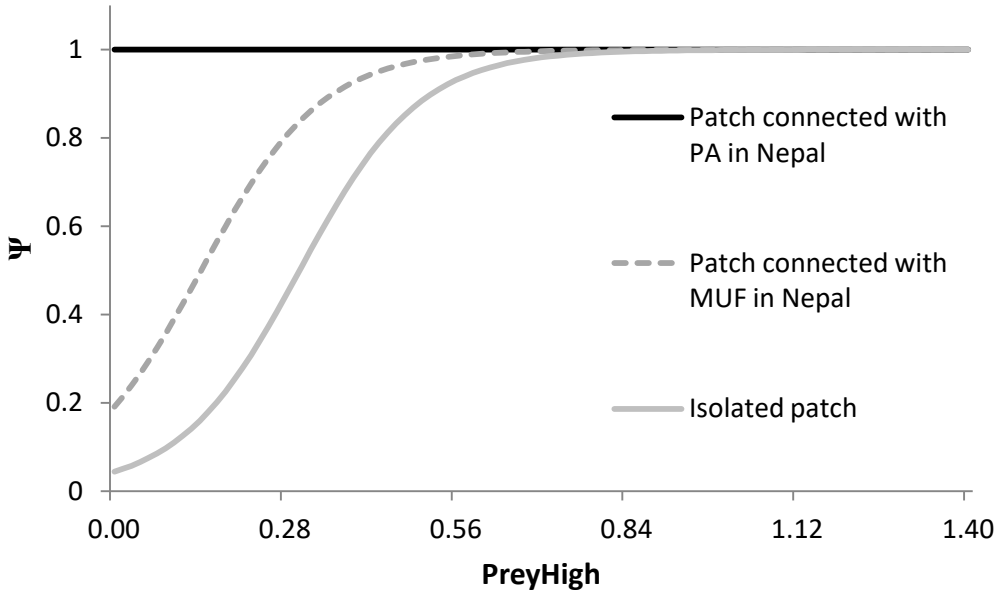

Figure 1 3. Relationship between large scale tiger occupancy (ψ) and prey relative abundance for cells within patches connected with MUFs in Nepal (MUF-Conn), patches connected with PAs in Nepal (PA-Conn) and isolated patches (No-Conn).

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Chapter 2: Modeling spatial heterogeneity in tiger density to assess the efficacy of tiger conservation in protected areas and multiple use forests

INTRODUCTION

Populations of large-bodied predators have declined worldwide and several species are functionally extinct in extensive areas of their range (Ripple et al. 2014, Check 2006). Large carnivore declines have profound direct and indirect impacts on ecosystem structure and function (Duffy et al. 2007, Dobson et al. 2006). A key conservation goal is to foster conditions that promote stable or growing populations of imperiled species. To devise appropriate strategies to meet these goals, it is important to investigate ecological and anthropogenic factors that cause spatial variation in key demographic parameters, such as density (*D*) and abundance (*N*) (Boyce and McDonald 1999, Burton et al. 2011) . Our ability to reliably estimate population parameters and link these to underlying environmental drivers is, in turn, dependent on the design and implementation of robust monitoring programs at appropriate spatial and temporal scales (Nichols & Williams 2006).

The distribution and abundance of organisms in space and time is intrinsically heterogeneous. Variations in densities of large carnivores have been attributed to multiple endogenous and exogenous factors (Vanak et al. 2013, Carbone and Gittleman 2002). Most relevant may be the availability of key prey species and distribution of sympatric competitors which are themselves patchily distributed (Bhola et al. 2012, Harihar et al. 2011, Carbone et al. 2011). Further, the location and availability of habitats for raising young, or areas secure from human threats, may strongly influence abundance and distribution of many large terrestrial

carnivores (Riley & Malecki 2001; Oriol-Cotterill et al. 2015; Chanchani et al. 2016). Terrestrial carnivores may also select for or against habitat edges; various large carnivores have been reported to exploit or avoid agricultural areas and other habitats with high levels of human disturbance (Harihar et al. 2009; Athreya et al. 2013), perhaps balancing prey availability against human threats (Basille et al. 2009). Physical features including water bodies and rugged topography and patch connectivity may also constrain animal movement and strongly influence space use (Dickson et al. 2005, Harihar and Pandav 2012). Human use of wildlife habitats, protection from poaching, and habitat management can also influence the demography and distribution of large carnivores (Kerley et al. 2002; Laliberte and Ripple 2004). Finally, endogenous factors including territoriality, mating systems and dispersal are key drivers affecting the distribution and abundance of carnivores, often an expression of density-dependent effects (Smith 1993, Carter et al. 2015).

Modeling and mapping patterns of spatial variation in species abundance and relating this variation to underlying causes is especially relevant for tigers, an imperiled species at high risk of local extinctions (The World Bank 2011, Wikramanayake et al. 2011). Recent studies using capture-recapture methods have revealed that tiger densities vary dramatically at both broad (across nations, landscapes and individual protected areas) and fine (locations within a contiguous habitat patch, such as within a single PA) spatial scales (Jhala et al. 2016; Chanchani et al. 2014b). Previous macroecological studies have documented that the persistence of wild tigers is critically linked to maintaining sufficiently high prey densities (Karanth et al. 2004, Chapron et al. 2014). but factors affecting fine-scale variation are less well known but needed for effective management and species recovery efforts.

The relationship between tiger and prey densities, though of obvious importance, may be less informative for tiger conservation and habitat management at fine spatial scales because prey abundance estimates are often referenced to large areas (Jathanna et al. 2003 ; Karanth et al. 2004). Recent studies that have modeled variation in tiger prey density at fine spatial scales have revealed that there may be steep gradients in the abundance of ungulate species, even within contiguous habitat patches, because of underlying variations in habitat quality or management (Harihar et al. 2014; Kumar 2010). One implication of such pronounced heterogeneity in prey abundance is that realized tiger densities may be considerably lower than predictions based on available habitat area and extrapolated (i.e., not spatially explicit) estimates of prey abundance.

Studying tiger-prey relationships may be incomplete without concurrent investigations of habitat attributes, such as the structure and composition of forests that drive the occurrence and abundance of tigers and their prey. In general, effective habitat management for tigers requires maintaining high productivity of palatable forage species in the understory to sustain high ungulate biomass, and retaining sufficient cover (Shrestha 2004, Sunarto et al. 2012, Dinerstein 1979). These important aspects of tiger-habitat associations have not been widely incorporated into management plans for protected areas or working plans of multiple use forests in India. Since the colonial era, large tracts of tiger habitats in India have been managed as timber-producing Reserve Forests, focused on optimizing production of commercially valuable timber species. In recent decades, several Reserve Forests have been gazetted as protected areas in which wildlife protection is prioritized, and logging is prohibited. Consequently, several PAs in India are now dominated by expansive tracts of homogenous, dense, closed-canopy These Sal (*Shorea robusta*) forests, with poorly developed understory -- essentially "green deserts" -- which support low densities of grazing ungulates (Seidensticker et al. 2010). In contrast, the

canopy cover is sparser in many current-day Reserve Forests which continue to be selectively logged. However, managers in Reserve Forests continue to expand forest areas, often by converting grasslands into timber-supplying woodlands, or granting grazing rights in such habitats. The influence of these contradictory management practices on tiger density merits scrutiny.

Previous studies have also emphasized that human use of landscapes negatively impacts tiger occurrence (Harihar and Pandav 2012, Barber-Meyer et al. 2013, Karanth et al. 2011). This assumption forms the premise for the designation of core (interior) and buffer (edge areas with high human use) zones in PAs. Such zonation is a cornerstone strategy for tiger conservation (Panwar 1982; Nyhus and Tilson 2004). However, recent studies indicate that tigers may extensively use edge habitats, provided that these areas support high prey densities and adequate cover (Chanchani et al. 2016). This suggests that the delineation of core and buffer areas on the basis of proximity to edges alone --without consideration of prey occurrence and abundance and habitat quality -- may not provide effective segregation of tigers and humans, as is desired in PAs.

Using two years of camera trap data from intensive sampling of tiger populations in several protected areas (PAs) and multiple-use forests (MUFs) in the Central Terai landscape (CTL) in North India, we sought to investigate how prey, habitat features and proximity to edges influence spatial heterogeneity in tiger density at fine spatial scales. Overall, we envisaged that at broad spatial scales (such as a habitat patch or an entire PA), the distribution and abundance of prey and habitat connectivity, rather than protection designation (i.e., protected area or multiple use forest), would explain spatial heterogeneity in tiger density. This prediction arises from our occupancy sampling study(Chanchani et al. 2016), and challenges the view that the species

persistence requires prioritized protection of 'source' populations resident in protected areas alone (Walston et al., 2010). We had four specific hypotheses. First, we predicted that prey density would be the single most influential predictor of spatial variation in tiger density. Second, we hypothesized that grasslands and forests with relatively sparse canopy cover would be associated with high tiger densities, relative to closed-canopy forests. Third, we hypothesized that the designation of core and buffer zones on the basis of distance to habitat edges would not accurately describe tiger abundance in the CTL. Finally, we predicted that spatial variation in the placement and extent of the sampling frame in multi-season camera trap surveys would yield estimates that are either biased or too imprecise to provide reliable insights about population trends. We tested these hypotheses by linking our camera trap data to capture-recapture models that provide statistically robust estimates of abundance, density and detection probability for wide-ranging, rare and highly mobile species (Borchers & Efford 2008; Karanth et al. 2011b; Royle et al. 2013). We tested ecological hypotheses about heterogeneity in tiger density in PAs and MUFs, using homogenous and inhomogeneous spatially explicit capture recapture (SECR) models that incorporated sex-specific heterogeneity in capture probabilities (Efford and Fewster 2013; Sollmann et al. 2011b).

METHODS

Study Area

The Central Terai Landscape (CTL, Fig 2.1), spans 5400 km^2 of lowlands and small mountain ranges abutting the lower Himalayan Ranges in the states of Uttarakhand and Uttar Pradesh in India and South West Nepal. The CTL is recognized as a globally important eco-

region and harbors numerous species of endemic and endangered plants and animals (Olson & Dinerstein 1998) including populations of tigers, hog deer (*Axis porcinus*), swamp deer (*Rucervus duvaucelii*), rhinoceros (*Rhinoceros unicornis*), and elephants (*Elephas maximus*) . Key vegetation communities are deciduous forests dominated by Sal (*Shorea robusta*) and grasslands characterized by *Saccharum spontaneum*, *Themeda arundinacea* and *Imperata cylindrica* (Dinerstein 1979, Johnsingh et al. 2004). The grasslands of the CTL are the region's most important habitats for imperiled large mammals; however, these habitats are now greatly reduced in extent because of agricultural expansion and associated growth of human settlements (Peet et al. 1999, Johnsingh et al. 2004). Today, the CTL is one of the most densely populated regions of Asia. Regions that have escaped extensive human transformation occur within the floodplains of the Sharda, Ghaghra and other rivers that flood annually during the monsoons.

Our study area included three PAs and three MUFs within The CTL (Fig., 2.1, Table 2.1). The three PAs (a national park and two wildlife sanctuaries) were established between 1972 and 1977 and are collectively known as Dudhwa Tiger Reserve. Management emphasis in Tiger Reserves like Dudhwa is to maintain inviolate habitats for tigers and other wildlife. In contrast, the CTL's three multiple use forests have experienced timber harvest, via selective felling, for ~ 150 years, and these areas are extensively used by local communities who extract fuel-wood, fodder and other resources (Strahorn 2009). The three MUFs lie within the largest patch of contiguous primary forest and grassland habitats in the CTL -- Pilibhit Forest Complex (PFC, 1400 km^2). The largest MUF within PFC, Pilibhit Forest Division, was accorded the status of Tiger Reserve (PA) in 2014 in recognition of its potential to sustain a viable tiger population. Within the CTL, one PA, Dudhwa National Park, is virtually isolated and only has

tenuous connectivity with other tiger habitats, while the other PAs and MUFs are connected with tiger habitats in Nepal via corridors (Fig 2.1; Chanchani et al. 2016).

Field Sampling

Camera trapping was conducted from November 2011 - June 2012 in the three PAs. Between November 2012 and June 2013 we re-sampled these three PAs and the 3 MUFs in the Pilibhit Forest Complex. Each area for which we derived separate estimates of density is referred to as a "site" (Table 2.1, Fig 2.1). All five sites were sampled in a period of ≤ 60 days to address the assumption of demographic closure for closed-population capture-recapture analysis (Karanth and Nichols 1998, Royle et al. 2009)(Table 2.1). We note that our definition of site does not necessarily mirror the administrative boundaries of PAs and MUF's in the region. Rather, the boundaries of a single site may encompass multiple adjacent PA's and or MUFs that were sampled within the 60 day 'closure' period.

Each camera trap station consisted of a pair of camera traps housed in metal security cases and secured to a post or tree 6 -10 m on either side of a forest trail or unpaved road, about 50 - 60 cm above the ground. Camera trap stations within the survey grid were spaced 1-2 km apart. To maximize the probability of capture, specific camera locations were based on extensive foot surveys and records of tiger track locations. The majority (>90%) of our cameras (models Cuddeback Attack, Reconyx Hyperfire or Spy Point FL-A) were equipped with a conventional "white" flash, while the remainder had infra-red flashes. We collected data from camera traps every 3-5 days.

Generally, we had too few cameras to survey a site in its entirety using a single trapping block. Therefore, we employed an incomplete trap layout design (Karanth and Nichols 2002, O'Brien and Kinnaird 2011), and sampled large sites using 2-3 trapping blocks. Each block of camera

trap stations was active for 15 - 30 days, after which cameras were shifted to an adjacent block (Table 2.1). Because more resources were available in the second year, sampling effort was higher in 2013 than in 2012 in terms of the number of camera trap locations. In Katerniaghat WLS, we sampled 30% more area in 2013, relative to 2012. In DNP, a marginally larger area was sampled with camera traps in 2013, relative to 2012 (Fig 2.1).

Identifying Individual Tigers

Photographs of adult tigers (>2 years of age) from camera traps were assigned to an individual tiger by three independent observers, based on pelage patterns. In addition, we also used a pattern recognition software (Extract Compare, Hiby et al. 2009) to aid in the identification of individual tigers. Individual identities from the two methods agreed perfectly. A photo-library of all individual tigers can be accessed online (Chanchani et al. 2014b). Site- and year-specific capture history matrices comprised of information on each tiger capture, were referenced to a specific trap station (location) and sampling occasion (24 hour period). In all, we compiled eight capture history matrices. Six of these were for the three PAs, which were sampled 2012 and again in 2013. The remaining two were for Pilibhit Forest Complex, the largest contiguous habitat tract, and Pilibhit Forest Division, the study area's largest MUF respectively. The PFC dataset comprised of tiger capture histories from Pilibhit Reserve Forest (a MUF), Kishanpur WLS (a PA) and the South Kheri & Surai MUFs, all of which were sampled within a 60 day (closure) period.

Overview of SECR Analysis

A key limitation of traditional estimators of animal abundance and density is that the area over which the "superpopulation" of the focal species is distributed is often unknown or estimated using ad-hoc procedures (Obbard et al. 2010, Ivan et al. 2013). However, recently

developed spatially explicit capture recapture models (SECR) provide reliable estimates of density (*D*) by estimating the locations of individual activity centers based on animal movement within the trap array (Borchers and Efford 2008, Royle et al, 2013, Efford et al. 2015).

In SECR models, the probability model for detection histories includes parameters for the distribution of home range centers (both within and beyond the trap area), and for detection probability, which is assumed to decline with increasing distance from an animal's activity center to a trap. The detection probability is typically modeled as a function of two parameters -- a scale parameter (σ) and the baseline detection probability (g_0), the probability of detection assuming that a camera trap lies at the individual's activity center (Efford et al. 2009). Because individuals within a population may scale the environment differently (e.g. male tigers have larger home ranges than female tigers), g_0 and σ may covary. In such cases, reliable estimates may be obtained by substituting the conventional detection parameterization g_0, σ by an alternate 'compensatory heterogeneity' parameterization a_0, σ (Efford & Mowat 2014).

In SECR analyses, the distribution of animal activity centers may be described by a homogenous or an inhomogeneous point process. Homogenous implies that the intensity of the point process is uniform across the region of integration, whereas an inhomogeneous point process implies that intensity varies across space, often as a function of environmental covariates (Efford & Fewster 2013). Model parameters can be estimated using likelihood or Bayesian methods (Efford et al. 2009; Royle et al. 2013).

Modeling Detection Parameters and Sex-Specific Capture Heterogeneity

We used SECR analyses (implemented in the R package SECR, version 2.9.5; Efford 2015) to test our hypotheses about spatial heterogeneity in tiger density (Table 2.2). We assumed that the distribution of tiger activity centers followed a Poisson point process (Efford & Fewster

2013). Following Royle et al. 2009, we defined the integration region (*S*) over which putative tiger activity centers could be distributed, by generating a grid of evenly spaced points (580 * 580 m^2) over primary tiger habitats (forest and grassland areas) in the CTL. Each of these points (encompassing an area of 0.34 km^2) represented a potential activity center for tigers in the sampled population. Estimates of density are based on the estimated number of activity centers within the integration region, S (Table 2.1). The region *S* consisted of a 15 km buffer around the trapping array at each site. We had previously ascertained a buffer of this extent was sufficiently large to contain the activity centers of all tigers exposed to our camera traps (Chanchani et al. 2014).

We estimated tiger density for each site (Table 2.1) using a two-step procedure in a multi-model hypothesis testing framework (Doherty et al. 2010, Burnham and Anderson 2003). First, we assessed relative support for six models with alternate parameterizations of the detection parameters (g_0 and σ, or a_0 and σ) with and without sex-specific heterogeneity (Figure 2.2). In most large carnivores, male home range sizes are larger than those of females (Sollmann et al. 2011, Smith 1993). To account for these differences, we allowed detection parameters to vary by gender using a two-class hybrid mixture model (Efford 2014). This hybrid mixture model includes a mixing proportion parameter 'pmix', which enables class-specific modeling of detection parameters and estimation of the sex ratio. We hypothesized that σ would be larger for male tigers (larger territory sizes) while g_0 would be larger for females (smaller territory sizes) and more restricted movement when caring for young; model $[g_0(sex)\sigma(sex)]$. Further, we tested three other models: common detection parameters for all individuals $[g_0(.)\sigma(.)]$ and sex-specific heterogeneity with respect to g_0 or σ [model structures $g_0(sex)\sigma(.)]$ and $[g_0(.)\sigma(sex)]$. Finally, we evaluated support for the compensatory heterogeneity parameterization (a_0, σ) by building two

additional models $[a_0(.)\sigma(.)]$ and $[a_0(.)\sigma(sex)]$ (Efford & Mowat 2014). For all 6 models, we retained a 'global' structure for density, allowing it to vary as a function of four covariates: distance to large (>1km^2) grasslands, percentage of tree canopy cover, prey density, and distance to nearest habitat (i.e., *D*(grass+treecov+prey+edge)). Relative support for models was assessed using Akaike Information Criteria (AIC) adjusted for small sample sizes (Burnham & Anderson 2010). The best supported model (lowest AICc score) from each model set was selected and carried forward into the second analysis step.

Density Estimation and Evaluating Hypotheses about Spatial Variation in Tiger Density

Retaining the best supported covariate structure for the detection parameters from step one, we built models to estimate tiger density (*D*). To each of our eight data sets we fit 15 models that represented our a priori hypotheses about the relative influence of prey density, habitat (vegetation cover) and proximity to edges on fine scale spatial variations in tiger density (Appendix 2.3, Table A5). We compiled values for five key covariates (prey abundance, distance from grasslands, percent tree cover, distance to forest edges and distance to the international border) for each point, representing a 580 m *x* 580 m (0.34 km^2) area over the integration region (Table 2.2).

We expected that prey density would be the strongest predictor of fine scale heterogeneity in tiger densities (Karanth et al. 2004). We derived spatially explicit estimates of prey density from line transect surveys (Chanchani et al. 2014b) using distance-to-detection data to estimate detectability (Buckland et al. 1993). Sparse detections of several ungulate species (e.g., swamp deer) precluded species-specific modeling of detection probability and density. Instead, we combined detection records for seven ungulate species -- chital, wild pigs, nilgai, hog deer, swamp deer, barking deer and sambar -- and estimated the cumulative detection probability

and density for all seven species across the CTL using Distance analysis (Appendix 2.1). Subsequently, we modeled spatial heterogeneity in ungulate density as a function of environmental covariates , while accounting for imperfect detection, using density surface models (Miller et al. 2013). These spatially explicit estimates of prey density served as a covariate in our tiger SECR models.

Grassland habitats in the Terai sustain locally high densities of prey species and provide cover for tigers to rest or raise cubs (Sunquist 2010, Shrestha 2004). We calculated the distance to large grasslands by hand digitizing grasslands >1km^2 from remotely-sensed imagery, and hypothesized that tiger densities would be higher in and around large grasslands. We also predicted that regions of dense tree canopy cover associated with *Sal* (*Shorea robusta*) forests would support low tiger density because of low understory productivity and prey densities (Dinerstein 1980, Bhattarai and Kindlmann 2011). We compiled tree canopy data from remotely sensed global tree canopy cover database (Table 2.2).

Finally, we developed two covariates to test our hypotheses about tiger use of edge habitats (Table 2.2). The first of these was the distance from each potential tiger activity center to the nearest habitat edge (PA or MUF boundary). We expected inverse relationship between distance to edges and tiger density, because the CTLs most productive riparian habitats lie along habitat edges. The second 'edge covariate' was the distance to India's international border with Nepal. We predicted that tigers density would be low along the international border, a region of extensive human use of tiger habitats and ongoing poaching (Wikramanayake et al. 2010, Chanchani et al. 2014b). At the broad scale, our expectation was that tiger density would be high in sites that also have high prey density and good habitat connectivity, and the lowest in sites with sparse prey density and poor habitat connectivity.

Prior to implementing SECR analysis, we tested for correlations among the five covariates. The distance to international border covariate was excluded from analysis because it was strongly correlated with prey density (R=0.78). Correlations values were less than 0.5 for all other covariates. We assessed relative support for models using AIC adjusted for small sample sizes. Given that the areas surveyed with camera traps differed between 2012 and 2013 (particularly in Katerniaghat WLS), we sub-sampled data from 2013 to replicate survey effort (coverage) from previous years in order to disentangle sampling related changes in population estimates from true population changes (Appendix 2.5).

Estimating Abundance

We estimated the abundance of tigers (N , the number of activity centers) within the boundaries of PAs and MUFs that we had sampled using the *Region.N* function in package SECR (Efford & Fewster 2013). Abundance (N) is distinguished from density because we are making reference to the number of individuals within a broad administrative region such as an individual PA (Efford and Fewster 2013). The boundaries of these regions represent a subset of the overall areas within integration region (S) for each site (Fig., 2.1). We compiled and compared estimates of N for all 15 models, for all eight model sets (Fig., 2.3; Appendix 2.3).

We also estimated tiger abundance using conventional single-season, closed capture recapture models (Otis et al., 1978; Karanth and Nichols 1998). Our primary motivation was to estimate p^*, the cumulative capture probability over the study period, computed as $[1-(1-p)^n]$, where p is the per occasion capture probability, and n is the number of occasions. Estimates of $p^* \approx 1$ indicate a near-census of the sampled population (Gerber et al. 2014). Closed capture-recapture analysis was carried out using program MARK (White & Burnham 1999) Appendix 2.4).

RESULTS

We sampled tiger habitats using 929 camera trap stations (304 locations in 2012 and 625 locations in 2013). Camera traps were cumulatively active for a period of 22,658 trap nights. The mean inter trap distance was 1356 m (Table 2.1). Over the study duration, camera trapping yielded 1352 independent captures of 92 adult tigers (45 males, 44 females) and two individuals of unknown gender. Across the two years, average number of recaptures (i.e. number of times an individual was recaptured after initial capture) was 12.49 for adult male tigers (SD=15.70) and 9.33 for female tigers (SD=8.94; Table 2.3).

Modeling Heterogeneity in Detection Parameters

Model selection results from the first analysis step varied between sites and across years (Appendix 2.2). Sex-specific heterogeneity in the scale parameter $\sigma(sex)$ was supported in six of the eight model sets. Further, in two of the six models, the inclusion of the 'compensatory heterogeneity' detection parameter $[a_0(.), \sigma(sex)]$ was better supported than the conventional baseline encounter parameter $[g_0(.),\sigma(sex)]$. Compensatory heterogeneity implies a negative covariance between g_0 and σ among individuals of one or both sexes. This outcome is observed when the differences in the detection probability of an animal at various locations in its home range are directly proportional to the amount of time it spends at different locations (Efford and Mowat 2014). Finally, there was support for sex-specific heterogeneity on estimates of both g_0 and σ $[g_0(sex), \sigma(sex)]$ in only one of the eight model sets (Fig 2). Similarly the dot model $[\sigma(.), g_0(.)]$ was only supported in only one of the eight model sets. Model selection results and parameter estimates for global modeled to determine optimal detection parameter combinations are in Appendix 2.2 (Tables A1-A4).

Broad Scale Patterns of Tiger Density and Estimates of Detection Parameters

Site-and year-specific estimates of tiger density (individuals/ 100 km^2) from the homogenous model were the highest in Kishanpur Wildlife Sanctuary KWLS$\widehat{D}_{2012}$ = 5.45 (SE=1.29), KWLS $\widehat{D}_{2013}$ = 4.97 (SE=1.27), a PA with extensive habitat connectivity and high ungulate densities. In contrast, tiger density was the lowest in Dudhwa National Park, (DNP $\widehat{D}_{2012}$ = 2.05 (SE = 0.56) $\widehat{D}_{2013}$ = 1.88 (SE = 0.52)), an isolated PA with low ungulate densities. The other PAs and MUFs had intermediate tiger densities: Katerniaghat Wildlife Sanctuary (KGWLS $\widehat{D}_{2012}$ = 4.76 (SE=1.14), KGWLS $\widehat{D}_{2013}$ = 2.78 (SE=0.72)); Pilibhit Reserve Forest (PRF $\widehat{D}_{2013}$= 3.028 (SE=0.71)); and Pilibhit Forest Complex (PFC $\widehat{D}_{2013}$ = 3.4 (SE=0.51)) (Figure 3, Appendix 2.3). In the three sites surveyed both in 2012 and in 2013, estimates were up to two times higher in 2012 than in 2013, but less precise (Fig., 2.3, Table 2.4, Appendix 2.5).

Model averaged estimates of σ, the scale parameter, were approximately two times higher for male tigers (range: – 2084 - 6931.64m) than for female tigers (range:1847 - 2962 m), (n= 6 site/ year combinations; Table 2.4, Fig., 2.2). Estimates of σ were the largest both for males and females in Katerniaghat Wildlife Sanctuary, a site with equal sex ratios and low tiger density. In contrast, the lowest estimates of σ were recorded in Pilibhit Forest Division and Kishanpur Wildlife Sanctuary, where sex ratios were female-biased, and tigers occurred at relatively higher densities. Both σ and $g_{o/}$ a_0 estimates and their CI were very consistent across all 15 models assessed in each of the 8 model sets(Table 2.4). Estimates of σ were consistently higher in 2013, than in 2012, especially in Dudhwa National Park and Katerniaghat Wildlife Sanctuary where survey effort was greater in the 2013. (Table 2.1). In general, even relatively small changes in the area sampled may yield estimates that are biased, or too imprecise to reliably inform population

trend (Appendix A5). Specifically, when regions of a large habitat patch associated with high tiger densities were sampled, estimates tended to be biased high.

Fine-Scale Variation in Tiger Density

Our hypothesis that fine scale heterogeneity in tiger density could be explained by spatial variation in ungulate prey density (assessed at the same scale) was supported only in Dudhwa National Park (2013), where the model (D((prey)) had 85% of overall support (Appendix 2.3, Table A5). In Dudhwa, there is a steep gradient in prey density, high in the south and low in the north. In four of the remaining seven model sets (sites), *D(Prey)* contained >10 % of the model support. The distance to grassland hypothesis (model *D(Grass)* had strong support (w=0.48) only in the Katerniaghat Wildlife Sanctuary (2012). Katerniaghat's grassland habitats exist only in its eastern and southern reaches, whereas the remaining areas of the PA are dominated by dense, even-age deciduous forests. In other sites where grasslands were distributed more uniformly, the distance to grassland covariate received less support. Models with the percent tree cover and distance to habitat edge covariates (*TreeCov* and *Edge*) had less support than models with no covariates (dot model, D(.)) in seven of eight model sets. In the six of the eight model sets, the dot model had the most support. AICc weight for the dot model varied between 0.8 in Kishanpur Wildlife Sanctuary (2013) and 0.23 in Pilibhit Complex (2013) (Appendix 2.3, Table A5). In several sites, models with one or more covariates had similar support to the dot model. Because the addition of a covariate did not result in improved model fit, these models were deemed uninformative (Arnold 2010).

Inhomogeneous point process models had less support in most sites relative to the dot model, but the direction of the relationship (positive or negative) between tiger density and covariates generally concurred with our predictions (Appendix 2.3 Table A6). Prey density

positively influenced tiger density, whereas increasing tree cover, increased distance from grasslands and forest edges were all negatively associated with tiger density (Fig., 2.5).

Estimates of Tiger Abundance

The single largest tiger population in the CTL was recorded in the Pilibhit Forest Complex ($\widehat{N}_{2013}$= 50.54, SE=2.63). While > 80% of the overall area of PFC lies within MUFs, this habitat patch supports the highest prey densities in the CTL, and is also connected with a PA in Nepal (Fig., 2.1, Appendix 2.7). The single largest tiger population within PFC was recorded in Pilibhit Forest Division, a MUF ($\widehat{N}_{2013}$ = 25.22; SE= 1.71). The 200 km^2 Kishanpur Wildlife Sanctuary – which is the sole PA within PFC -- also supported a notably large tiger population ($\widehat{N}_{2012}$ =19.21; SE=1.54) and ($\widehat{N}_{2013}$= 16.0; SE = 0.02

In contrast, the CTL's flagship PA, Dudhwa National Park, supported a relatively small population of tigers ($\widehat{N}_{2012}$=14.25, SE = 0.51; $\widehat{N}_{2013}$=14.16, SE = 0.41). Dudhwa is similar in size to Pilibhit Forest Division, but is isolated, and large areas of the Park have very low prey densities. In Katerniaghat Wildlife Sanctuary, the estimated number of tigers was $\widehat{N}_{2012}$=19.21 (SE = 1.54) and $\widehat{N}_{2013}$=17.11 (SE =0.33) in 2012 and 2013, respectively. Katerniaghat is 40% smaller than Dudhwa National Park and the two PAs have similar (low) prey densities. However, Katerniaghat is connected with Bardia National Park in Nepal via the Khata corridor, whereas Dudhwa's connectivity with adjacent forests in Nepal has been severed in recent years. All estimates of abundance are model averaged, with the exception of those for Dudhwa in 2013, where a single model was well supported.

Estimated sex ratios for adult tigers were female-biased in Kishanpur WLS, but male-biased in Dudhwa NP and Katerniaghat WLS (Table 3). Finally, even though estimates of density were similar across the two years in several sites (e.g. Katerniaghat WLS, Dudhwa NP),

we note that there was a high turnover (~30%) of adult tigers, even in the span of a single year (for age and sex-specific details of tiger captures, see Appendix 2.6). The point estimates for the 15 models within each of the 8 model sets were consistent, and in general, and had similar precision (Fig., 2.3, Appendix 2.3, Table A5).

Estimates of abundance from the closed capture-recapture models in program MARK were similar to the abundance estimates from the SECR models (Appendix 4, Table A7). The cumulative detection probability p* (for model M_0) for all sites, ranged between 0.9 and 1.0, indicating that we likely achieved a near-census of populations through camera trap sampling (Gerber et al. 2014).

DISCUSSION

We found pronounced spatial variation in tiger density across the landscape at both broad and fine spatial scales. While the protection of tigers and other wildlife has been prioritized in PAs, surprisingly we found higher tiger densities in MUFs than in Dudhwa National Park, the CTL's flagship PA. We found that local variations in the abundance and distribution of prey , availability of productive habitats such as riparian grasslands best explained spatial variation in tiger densities. In addition, our results suggest that local variations in illegal hunting of prey, tiger poaching and degree of patch connectivity may all may contribute to spatial variation in tiger densities in the CTL. Finally, our study demonstrates that variations in the size of the camera trap array (area sampled) among years may negatively or positively bias estimates of species density and abundance, even when using SECR models. If the components of survey

design are not standardized, it is impossible to discriminate true population change from that attributable to design changes.

At broad spatial scales (such as a site or habitat patch), patterns of tiger abundance mirror the species occupancy patterns in the CTL. Previously, we documented that prey abundance, habitat connectivity and the presence of grassland refugia—rather than protection status (PA or MUF)—best explain patterns of tiger occurrence (Chanchani et al. 2016). Consistent with these findings, estimated tiger density was highest in Kishanpur WLS, an area with high prey densities in good habitat connectivity. Tiger densities were lower in Katerniaghat WLS, a protected area with low overall prey densities, but intact habitat connectivity. The lowest tiger densities in the CTL were recorded in Dudhwa National Park, an area with low prey densities and poor habitat connectivity. Importantly, the only administrative areas with populations > 25 adult females were in the PFC, composed primarily of MUFs where logging and high levels of day-time human are permitted. In contrast, PAs such and Dudhwa National Park and Katerniaghat WLS supported smaller tiger populations despite a legal mandate to prioritize tiger conservation. In all, our results reveal important deficiencies in current conservation strategies that emphasize conservation efforts primarily in designated PAs (e.g., Walston et al. 2010). Similar to other authors (Dinerstein et al. 2007; Wikramanayake et al. 2011), our results suggest that conservation efforts be extended beyond the borders of PAs to include the human-use landscapes that surround PAs.

At two sites (Dudhwa National Park and Katerniaghat WLS), we found evidence for strong relationships between environmental factors and fine-scale heterogeneity in tiger density. In Dudhwa NP, prey density varied extensively along a steep north-south gradient. The northern areas of Dudhwa support extremely low prey densities even though the area has extensive

grasslands and perennial water availability. Previously, we hypothesized that this was a consequence of high poaching pressure along the international border (Chanchani et al. 2014a; Fig., 2.1; Appendix 7). Our present study supports this hypothesis—we found a strong positive correlation between distance from the international (Nepal) border and prey density. In contrast, in the southern portions of Dudhwa NP prey densities were considerably higher and tigers densities were much greater. Dudhwa's small tiger population may be susceptible to extinction unless law enforcement is strengthened and key corridors in Nepal are restored. In Katerniaghat WLS, tiger and prey densities along the northern boundary are similarly low (Fig., 2.4, Appendix 7). The negative relation between distance to grassland and tiger density suggests that low tiger densities in large areas (northeastern portions) of this sanctuary are attributable to the absence of grasslands. In addition, in the past forest tracts away from the flood plains were intensely managed to promote *Sal* production. Under current management practices, which prohibit logging, these *Sal* forest tracts dominate the landscape. These forest are dense and homogenous with little vertical or horizontal heterogeneity, poor understory productivity and low prey densities (Shrestha 2004). Areas with relatively sparse tree cover appear to support higher tiger and prey densities (Fig., 2.5c)

Contrary to our expectations, prey and vegetation (grasslands, tree cover) covariates were generally weak predictors of spatial variation in tiger density in other sites. In contrast, a model with no covariates *[D(.)]* had the most overall support (six of the eight model sets for the complete analyses and two of the four subset analyses). However, we do not believe it is appropriate to conclude from these model results that these factors are unimportant. If the D(.) models were universally the best, we would not have observed pronounced spatial heterogeneity in tiger density (see Fig., 2.4 and Appendix 7). This begs the questions as to why our top models

generally did not include these covariates. At least two scale-relevant factors are important to consider. First, prey density and grassland patches vary at a spatial scale that is generally smaller than the average home range size of tigers. As a result, at our scale of covariate measurement, tiger habitat (and large territory sizes) use effectively smoothed over this heterogeneity, except in sites where the prey density gradient was strongly directional (eg. Dudhwa National Park, Fig., 2.4). Second, we note that while all sites within the study area had steep gradients in prey density, prey occurred at relatively higher density within large areas of PFC than they did in Dudhwa or Katerniaghat (Fig. 2.6) Finally, we speculate that the unique geography of the CTLs forest patches, some of which are very narrow (e.g. Pilibhit Reserve Forest) , may highly constrain tiger space use, and cause available habitats, whether productive or not, to be used (Fig., 2.1, Appendix 7).

The relationship between edge habitats and tiger space-use is complex, and "distance to forest edge" was not strongly associated with variation in tiger density. Edge habitats proximate to human settlements may support high tiger densities if these edges border productive riparian habitats or agricultural areas exploited by prey species (e.g., sugarcane and wheat fields). Smith (1993) found that tigers avoided the agricultural matrix around Chitwan National Park in Nepal, but more recent studies in India documented tigers use of agricultural areas (Athreya et al. 2013). Sugarcane plantations mimic natural tall grasslands and provide excellent cover and prey resources. During our study, we photo captured two female tigers that successfully raised cubs to adulthood in the agricultural matrix. Our results also suggest that the current designation of buffer zones and core zones in habitats lacks a scientific foundation and poorly reflects patterns of tiger occurrence and abundance. To effectively conserve tigers in these landscapes, we believe

it is essential to extend conservation actions into multiple use forests and the agricultural matrix that surrounds PAs and MUFs.

Our findings also have important implications for camera trap based monitoring of large carnivores. First, we found that it is important to model sex-specific heterogeneity in σ in order to reliably estimate density from SECR models (Sollmann et al. 2012). Strong support for sex-specific heterogeneity in σ was expected because male tiger home ranges are typically 3-4 times larger than those of females (Smith 1993, Harihar et al. 2009). Second, our study demonstrates that carnivore densities may be spatially inhomogenous, particularly in areas with steep environmental or disturbance gradients. As a result, extrapolation of tiger densities to areas considerably larger than the trapping grid (Jhala et al. 2010) is not justified. To reliably estimate population trend, the spatial and temporal boundaries of the sampling frame must remain constant (Reynolds 2012), otherwise true changes in population density are confounded by changes in the population sampled.

TABLES

Table 2.1. Details of camera trap sampling for tigers in the Central Terai Landscape (2012 and 2013)

Site	Protection designation	Area (km2)	Sampling period	Trap nights	Trap stations	Sampling blocks	mean inter-trap spacing (km)	Tiger Density, SE and CI**
2012								
Dudhwa NP	PA	700	Feb - Apr 2012	2626	159	3	1.78	2.05(0.56);1.21 - 3.48
Katerniaghat WLS	PA	443	Apr - June 2012	2190	82	2	1.37	1.55(1.26);0.39-6.24
Kishanpur WLS	PA	206	Dec - Feb 2012	2648	63	1	1.63	5.45(1.29);3.45 - 8.61
2012 subtotals		***1349***		***7464***	***304***	***6***		
2013								
Dudhwa NP	PA	700	Feb - April 2013	4861	202	2	1.42	1.93(0.92);0.8-4.7
Katerniaghat WLS	PA	443	November - Jan 2013	3663	111	2	1.52	2.87(0.72);1.78 - 4.65
Pilibhit Complex								3.4(0.51);2.54-4.56
Kishanpur WLS	PA	206	April - June 2013	2655	67	1	1.53	4.97(1.27);3.04-8.12

Pilibhit FD	MUF*	712	April - June 2013	2814	171	3	1.96	3.28 (0.71);2.16-4.98
South Kheri & Surai[++]	MUF*	452	April & June 2013	1201	74	2	2.63	
2013 subtotals		***2513***		***15194***	***625***	***10***	***9.06***	
TOTAL				22658	929	16	9.06	

[**] Estimates for all sites are model averaged, with the exception of DNP '13 for which the estimates are from a single well supported model *D(prey), w=0.85*.[++] We did not separately estimate density for South Kheri and Surai because of too few camera captures from these sites. These capture events were however included in the models for PFC. The five sites for which data were analyzed separately are: Dudhwa National Park, Kishanpur wildlife Sanctuary, Katerniaghat Wildlife sanctuary, Pilibhit Forest Division and Pilibhit Forest Complex. Trap nights computed by summing trap functionality of stations (i.e. pairs of camera traps).

Table 2.2. Details of covariates modeled to explain heterogeneity in tiger density. A point represents 0.336 km^2 (580 m x 580 m) over the integration region.

Covariate	Hypothesized relationship with tiger density and reference	Covariate preparation	Data source
Prey density (Prey)	Strongly positive (Karanth et al. 2004, Carbone and Gittleman 2002).	Combined estimates of prey density for 7 species derived for each point in the integration region using distance sampling and GAMs (Appendix 1)	Line transect sampling in the CTL conducted concurrently with tiger monitoring.
Percent tree cover (TreeCov)	Negative. Dense dipterocarp forests in the Terai are associated with low tiger and prey densities (Shrestha 2004, Bhattarai and Kindlmann 2011) but some studies have argued that densely forested areas provide optimal habitats for tigers (Kanagaraj et al. 2011).	Derived from remotely sensed data (MODIS global imagery, 250 m resolution).	Land Processes Distributed Active Archive Centre, USGS. https://lpdaac.usgs.gov/404/products%20modis%20products%20table%20mod44b. Accessed on December 12, 2014.
Euclidian distance (m) to large grasslands (Grass)	Negative. Grasslands provide cover and are also the preferred habitats of species such as hog deer and swamp deer (Smith et al. 1998)	All grasslands within the CTL were hand digitized from satellite imagery. Grasslands > 1 km^2 in area were retained for analysis.	Google Earth
Euclidian distance (km) to primary	Negative. Although ecological literature has argued that edges may be associated with reduced presence/ abundance of carnivores	Hand digitized database of forest and grassland boundaries.	Google Earth.

habitat (forest and grassland edges). (Edge)	because of high human disturbance (Bhattarai and Kindlmann 2013), Chanchani et al (2016) found no support for this relationship in their occupancy analyses in the CTL. Edges may be used extensively by tigers because such areas are associated with productive riparian habitats.	
Euclidian distance (km) to international border (IntBorDist)	Positive. Interviews with forest department personnel suggested that human pressures were high in CTL areas that bordered Nepal. Anecdotal information and literature indicate that the meat of wild ungulates is in high demand in Nepalese villages in the Terai (Paudel & Kindlmann 2012)	GIS data for political boundaries.

Table 2.3. Summary of photo captures of tigers from camera trap sampling in the CTL (2012 and 2013)

				Female			Male			gender unknown		
Site*/ year	Mt+1	Number of individuals with recaptures	Independent tiger captures	count	Sum	avg # of recaptures	count	sum	avg # of recaptures	count	sum	avg # of recaptures
Dudhwa NP '12	14	12	131	5	42	8.40	9	84	9.33			
Katerniaghat WLS '12	18	15	88	7	35	5	11	53	4.82			
Kishanpur WLS' 12	19	16	264	11	119	10.8	8	143	17.17			
Dudhwa NP '13	14	13	274	7	92	13.1	7	182	26.00			
Katerniaghat '13	17	16	265	10	106	10.6	7	101	14.43			
Kishanpur '13	16	15	256	9	151	16.8	7	145	18.13			
Pilibhit Forest Division '13	23	17	94	11	43	3.91	10	49	4.90	2	2	1
Pilibhit Forest Complex '13	45	38	393	25	213	8.52	18	175	9.72	2	5	2.5

Table2. 4. Model averaged estimates of sex-specific detection parameters (σ and $g_{0,}$) for all sites sampled in 2012 and 2013. M and F are notations for male and female tigers respectively, and bold values indicate sex-specific differences in g_0 or σ.

Site and year*	go F(se)	go F (CI)	go M(se)	go F (CI)	σ F (se)	σ F (CI)	σ M (se)	σ M (CI)	pmixM(se)	Pmix (CI)
DNP 12	0.04 (0.01)	0.03-0.05	0.04 (0.01)	0.03-0.05	**2340.33 (220.94)**	1945.8-2814.85	**4170.02 (318.61)**	4125.81-5376.96	0.58 (0.14)	0.31-0.81
KGWLS '12	0.04 (0.01)	0.03-0.05	0.04 (0.01)	0.03-0.05	2263.56 (189.73)	1921.19-2666.95	2263.56 (189.73)	1921.19-2666.95	0.61 (0.11)	0.38-0.8
KWLS '12	0.06 (0.01)	0.05-0.07	0.06 (0.01)	0.05-0.07	**1847.1 (101.6)**	1658.46-2057.2	**3991.83 (257.48)**	3518.24-4529.18	0.29 (0.1)	0.14-0.51
DNP '13**	0.04(0)	0.04-0.05	0.04(0)	0.04-0.05	**2812.87 (156.72)**	2522.09-3137.18	**4973.53 (205.43)**	4586.93-5392.72	0.47 (0.13)	0.24-0.72
KGWLS '13	0.05 (0.01)	0.04-0.06	0.05 (0.01)	0.04-0.06	**2962.19 (189.84)**	2612.87-3358.21	**6931.64 (373.55)**	6237.31-7703.27	0.33 (0.11)	0.16-0.56
KWLS '13	0.08 (0.01)	0.06-0.09	0.08 (0.01)	0.06-0.09	2083.56 (86.06)	1921.6-2259.17	2083.56 (86.06)	1921.6-2259.17	0.4 (0.13)	0.19-0.65
PRF '13	0.03(0)	0.02-0.03	0.03(0)	0.02-0.03	**2294.52(232.29)**	1882.52-2796.69	**3752.97 (350.57)**	3126.33-4505.21	0.37 (0.1)	0.2-0.59
PFC '13	**0.07 (0.01)**	0.05-0.08	**0.03(0)**	0.02-0.04	**1857.38 (85.65)**	1696.96-2032.96	**4170.3 (222.14)**	3757.15-4628.89	0.35 (0.07)	0.23-0.5

* DNP: Dudhwa NP, KGWLS: Katerniaghat WLS, KWLS: Kishanpur WLS, PRF: Pilibhit Reserve Forest, PFC: Pilibhit Forest Complex

** Estimates for DNP (2013) are not model averaged and are instead from a single well supported model (*D(prey)*, w=0.85)

FIGURES

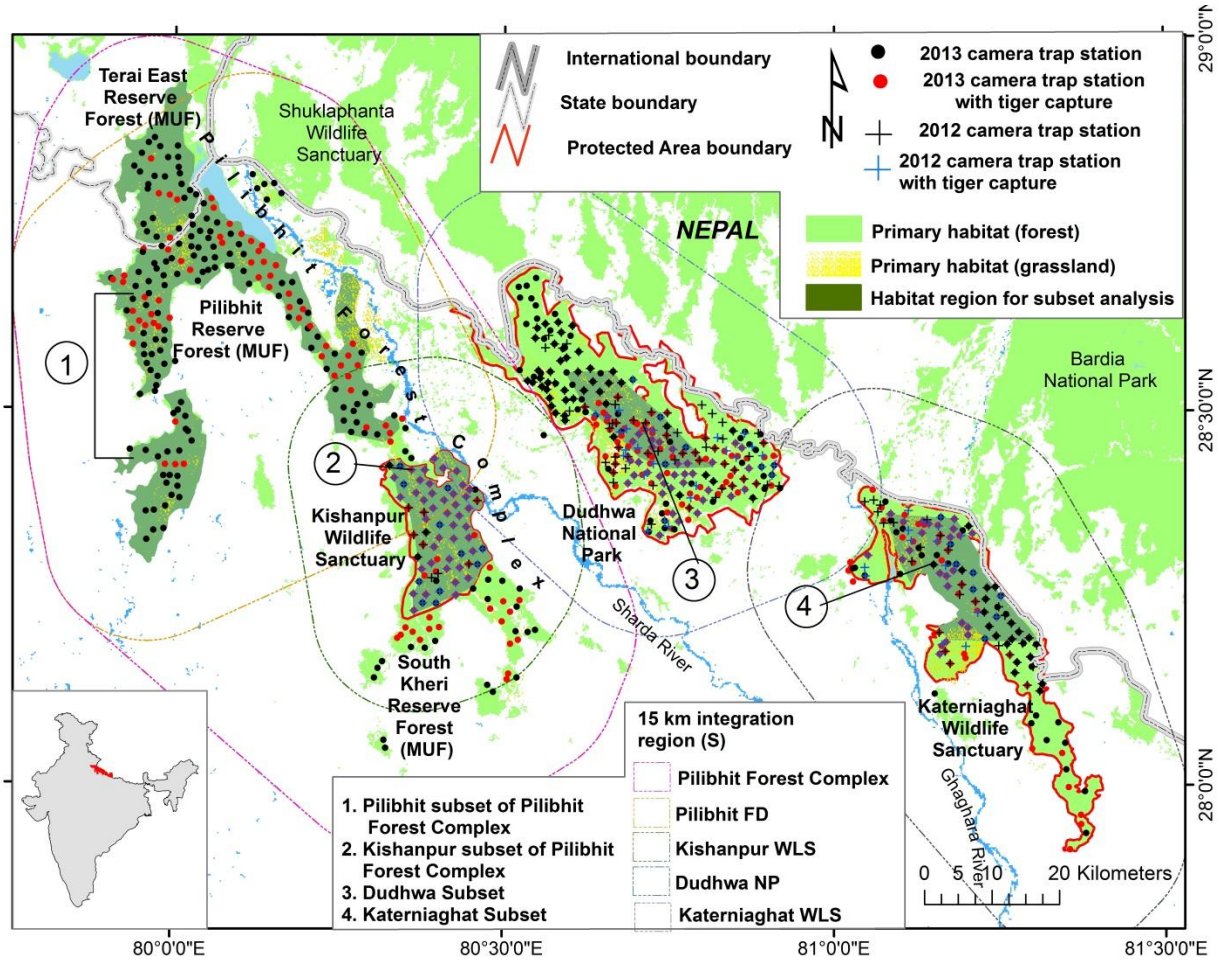

Figure 2.1. Map of the Central Terai Landscape depicting locations of camera traps, with and without tiger captures in 2012 and 2013. The region of integration associated with each 'site' subject to SECR analysis are depicted as polygons. The region of integration was delineated using a grid of evenly spaced points each of which represented an area of 0.336 km^2. Points that intersected 'habitat' were all assigned covariate values, whereas points in non-habitat areas were masked-out from the analysis.

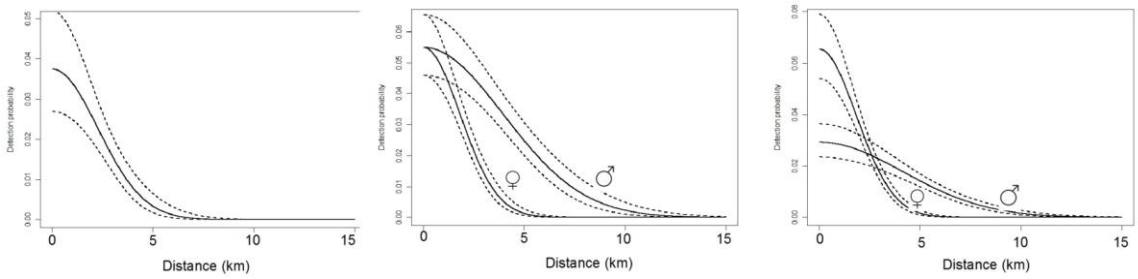

Figure 2.2. Representative detection function plots for 3 scenarios (a) no sex-specific heterogeneity in σ or g_0; (b) sex-specific heterogeneity in g_o only; and (c) sex-specific heterogeneity in both σ and g_o.

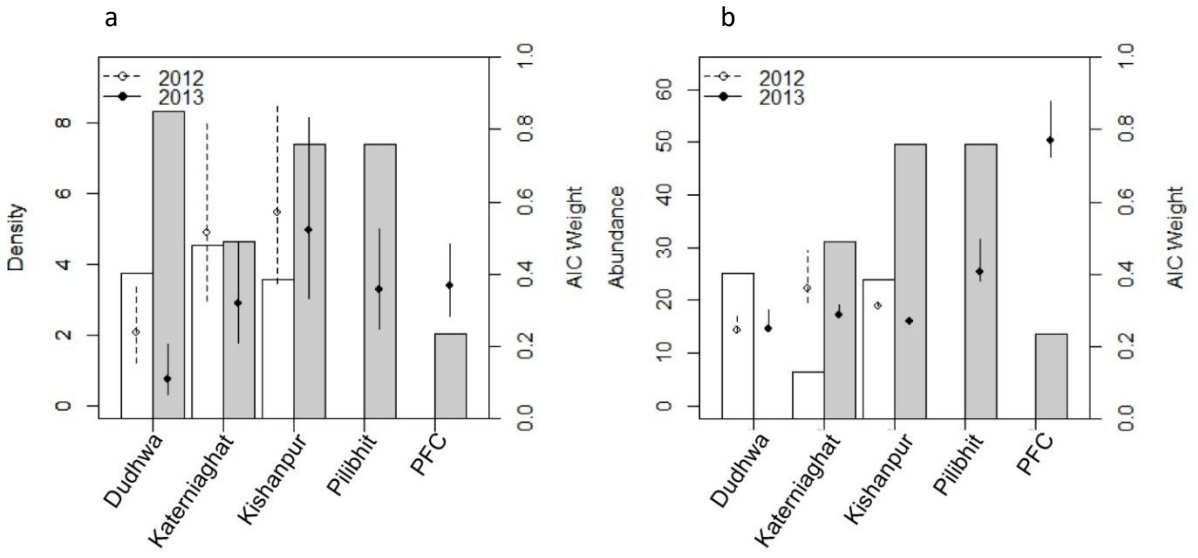

Figure 2.3. (a) Point estimates of tiger density (individuals/100 km^2), (b) abundance, and associated 95% confidence intervals for the CTL (note difference in scale on y-axes). Separate estimates are provided for the 5 sites sampled in 2013 and 3 sites in 2012. Empty and filled bars provide estimates of the AICc weights (model support) for 2012 and 2013, respectively. All estimates are from the best supported model for each site/ year. The D(.) model was the best supported model, with the exception of $Katerniaghat_{2012}$ D(Grass) and DNP_{2013} D(Prey).

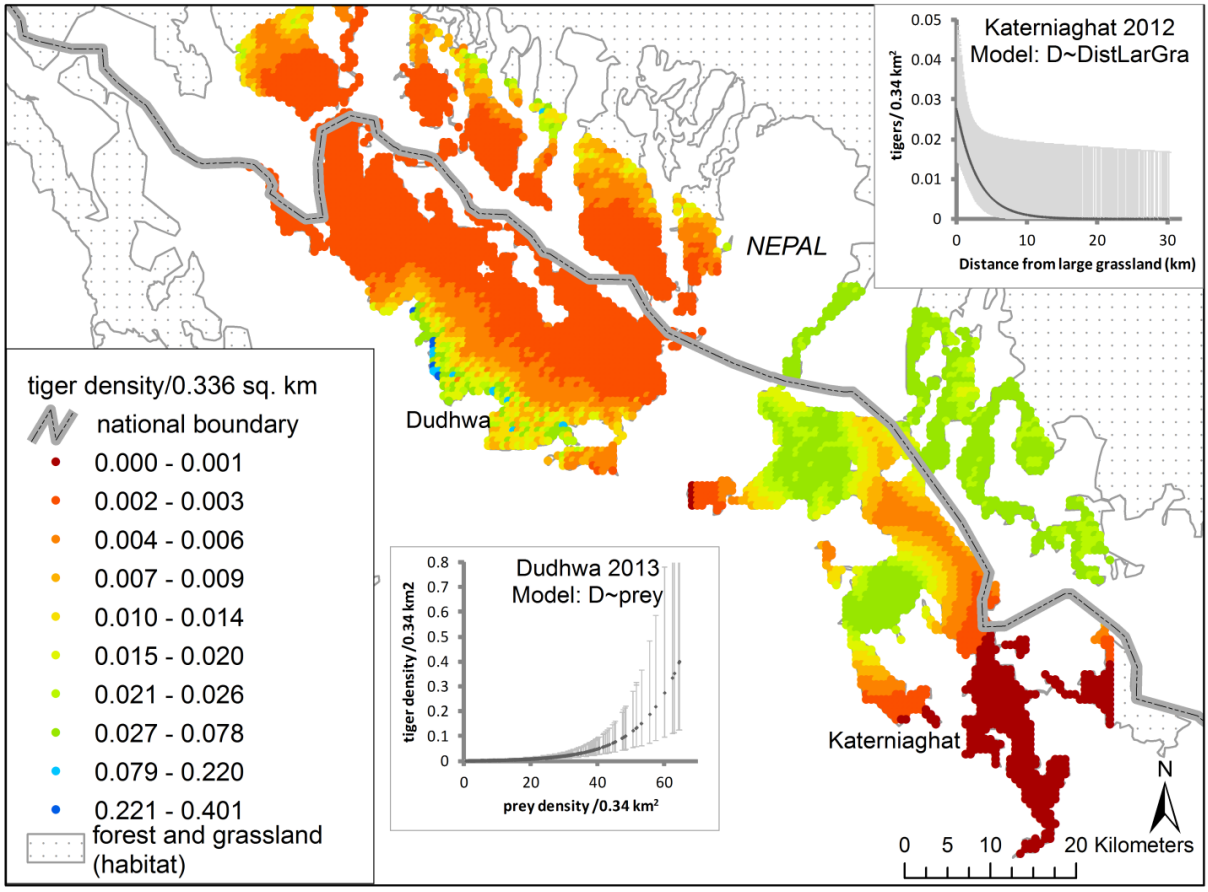

Figure 2.4. Density surface output for Dudhwa National Park and Katerniaghat Wildlife Sanctuaries. Inhomogeneous point process models D ~ f(prey) in DNP 2013 and D ~ f(distance to grasslands) in Kateriaghat 2012. Each point on the map represents a habitat area of 0.336km^2 within the integration regions of Dudhwa and Katerniaghat, respectively. Cool shades (blues and greens represent areas with higher tiger densities, warm shades (yellows and reds) represent areas of low density. Covariate relationships with tiger density for the two sites, and associated 95% confidence intervals have also been plotted.

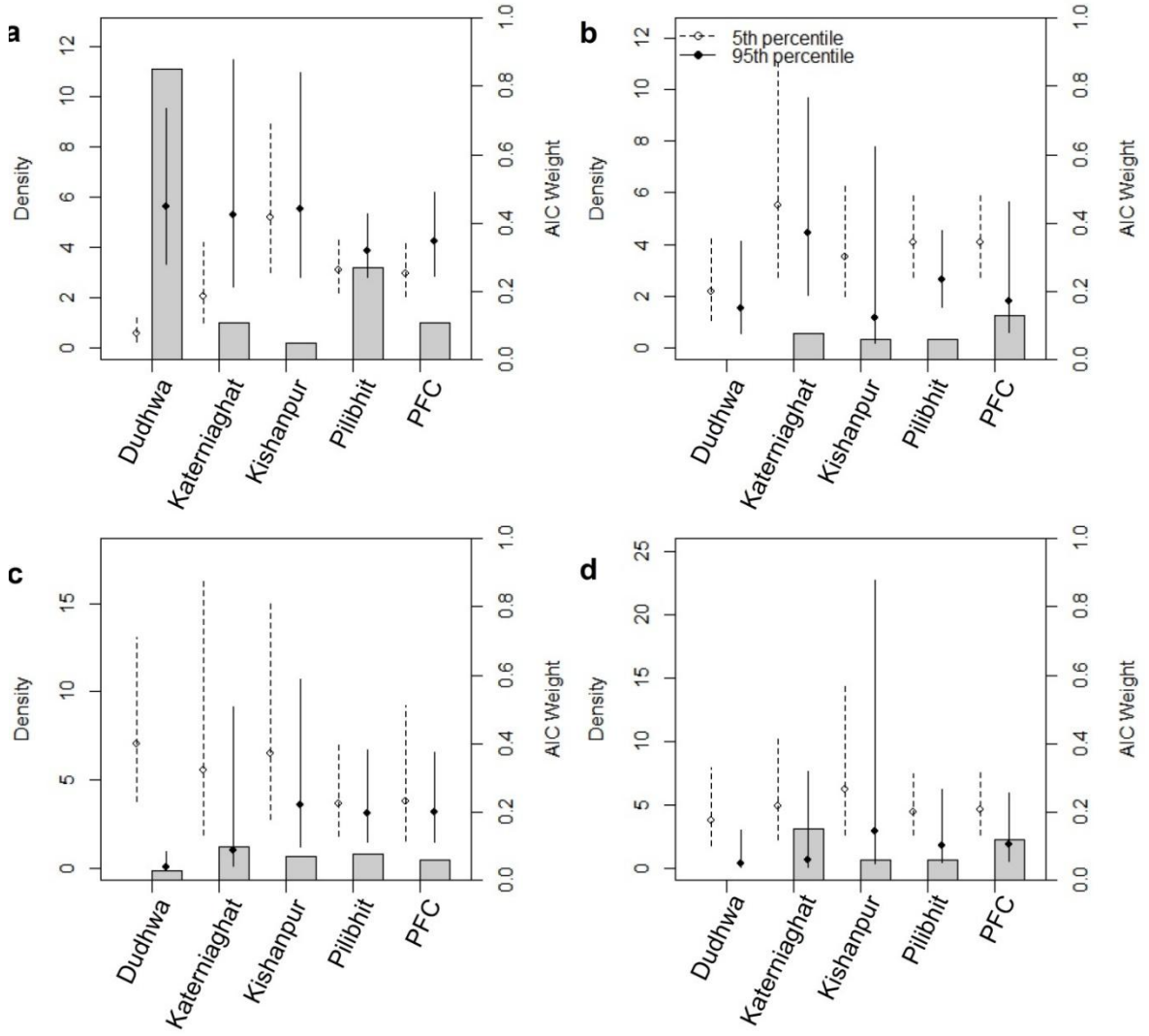

Figure 2.5. Estimates of tiger density for five sites in the CTL (2013 data) from modes representing our four key hypotheses (a) prey density; (b) distance to large grasslands; (c) percent tree cover and; (d) distance to habitat edges. Hollow circles and dotted error bars represent tiger densities and 95% confidence intervals associated with minimum covariate values (5th percentile), whereas solid circles and error bars are estimate of density and associated 95% confidence intervals near the upper boundary of covariate values (95th percentile). Gray bars (secondary y-axis) depict AIC weights associated with the models.

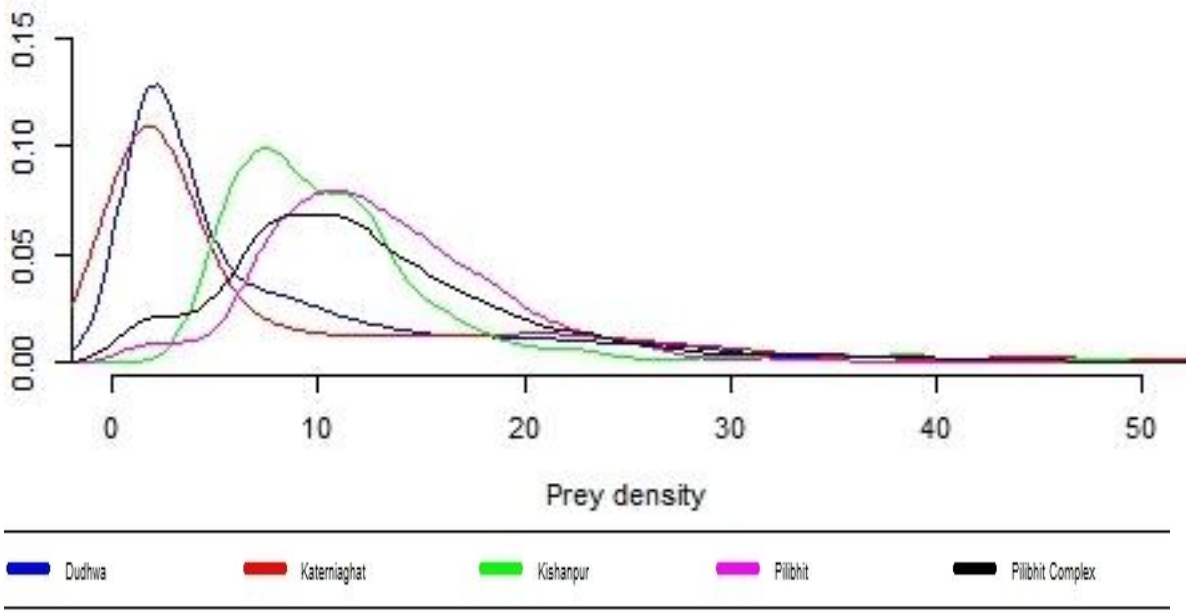

Figure 2.6. Distribution of prey density in the CTL's 5 study sites. The prey covariate had relatively higher support in inhomogeneous density models for Dudhwa and Katerniaghat, in which a large proportion of the overall area is associated with low prey densities, and relatively small areas have high prey densities. In contrast, relatively large areas of PFC, Pilibhit Reserve Forest ad Kishanpur wildlife sanctuary were associated with higher prey densities.

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Chapter 3: High potential for intraspecific competition in small tiger populations occupying fragmented landscapes

INTRODUCTION

Adult sex ratio (ASR, male: female) is an important demographic parameter that influences both individual behavior and population dynamics (Caswell 2001; Le Galliard et al. 2005; Haridas et al. 2014; Székely et al. 2014). Skewed or uneven sex ratios in animal populations can occur for a variety of reasons, including sex differences in survival due to disproportionate costs of reproduction for females and sex-biased immigration or emigration by males (Veran & Beissinger 2009). It has been hypothesized that ASR in many species may also be an artefact of intrasexual competition, which can result in increased mortality or dispersal of the sex with higher frequency in a population (Clutton-Brock et al. 2002; López-Sepulcre et al. 2009). Male-biased sex ratios may result in increased aggression by males towards females, resulting in a decline in their fecundity and survival with negative effects on population growth and persistence (Le Galliard et al. 2005; Grayson et al. 2014; Barrientos 2015).

In polygamous species, adult male territories often encompass the territories of multiple females. Skewed ASR's have especially pronounced impact on the behavior and demography of carnivores—for example, intraspecific cannibalism has been documented in at least 14 large carnivore species (Polis 1981). In species where cannibalism is frequent, the prevalence of 'cannibalistic genes' may reduce overall population fitness, or result in high rates of mortality that may eliminate entire generations or cause populations to become locally extinct (Polis 1981). When first acquiring a female territory, adult male carnivores are known to seek out and

kill non-related juveniles to increase their reproductive fitness (Hrdy 1979; Persson et al. 2003; Barlow et al. 2009). Additive mortality from intraspecific competition and infanticide may be especially detrimental for small populations of several terrestrial carnivores that are extremely vulnerable to extinction (Chapron et al. 2008)**.**

Large carnivores worldwide face high extinction risks, in part because of their extensive area requirements, habitat loss and real or perceived conflicts with humans (Ripple et al. 2014). Tiger (*Panthera tigris*) populations are especially at risk because of a lucrative illegal global trade in their pelts and other body parts -- as few as 3900 individuals may now exist in the wild (WWF 2016) and remnant populations are small with fewer than 20 populations >50 individuals. While the risk of local extinction is primarily driven by illegal hunting and habitat loss and fragmentation, several endogenous factors may exacerbate extinction risks of small populations. For example, strong territorial behavior can aggravate the demographic issues of small and fractured populations. Intraspecific competition and aggression, especially in areas with male-biased ASR can increase the extinction risks of small populations (Barlow et al. 2009). Adult male tigers fiercely defend their territories from competing males to retain access to breeding females (Sunquist 1981; Horev et al. 2012). If a dominant territorial male is displaced by a rival, the outcome is often infanticide of the former's cubs by the later (Smith & McDougal 1991; Barlow et al. 2009). The harem size of male tigers and degree to which breeding males are able to maintain stable territory sizes can profoundly impact population dynamics and extinction rates (Horev et al. 2012).

Several aspects of the social behavior of tigers, including territoriality and dispersal, are relevant to demography, behavior and space-use. Female tigers select territories to secure access to adequate resources to protect and raise young (e.g. sufficient prey, cover and water), and

males compete for territorial dominance of one or more female territories (Sunquist 1981; Smith 1993; Goodrich et al. 2008). In South Asia, male tiger territory size is usually >100 km^2, while females maintain territories between 10-30 km^2 (Sunquist 1981). Dispersal is also typically male-biased: adult females usually tolerate their female offspring establishing territories within or in close proximity to their own, but male offspring are aggressively driven away. Young males in search of new territories often disperse over large distances and commonly experience aggressive interactions with other males (Smith 1993; Reddy et al. 2016). Although published information is sparse, a ASR of 1:3 has generally been assumed in South Asia (Sunquist 1981). Recent studies in North India have revealed that densities and sex ratios of adult tigers can vary widely, and may even be male-biased (Chanchani et al. 2014b).

These results raise several questions relevant to tiger population ecology and conservation. First, do variations in ASR partially explain patterns of fine-scale habitat use (i.e., site-occupancy) by male tigers? Second, is there evidence for intense intraspecific competition in local populations with male-biased ASR? Lastly, can inter-site variations in ASR for tiger populations be attributed to sex-biased emigration, poor limited connectivity, or to differences in sex-specific survival rates?

To evaluate these hypotheses, we analyze an extensive capture-recapture dataset for a tiger population in Dudhwa Tiger Reserve (DTR)– a 1200 km^2 protected area within the Central Terai Landscape (CTL) in North India. DTR consists of three disjoint protected areas (subsequently referred to as, 'sites'). Sites are characterized by strong gradients in tiger density, habitat connectivity and variation in ASR—ranging from highly connectivity, high density and female-biased ASR—to isolated, low density and male-biased ASR. We tested the null hypothesis that the probability of habitat use (fine-scale occupancy) by one or more male tigers

would be similar, regardless of a site's ASR. Alternatively, we hypothesized that sites with male-biased ASR would be characterized by: (a) lower overall male habitat use, i.e., extensive habitat areas not used by male tigers because of the lack of females; (b) high probability of occurrence of a single male tiger in locations without females; and (c) high probability of multiple male tiger use of locations occupied by ≥ 1 female (Table 1).

Our hypotheses are based on three well-known aspects of tiger behavior: polygyny, aggressive defense of territories (and harems) by males, and obligate dispersal of juvenile males (Smith & McDougal 1991; Smith 1993). Territorial behavior strongly influences space use, and the distribution of individuals in a landscape. As the density of adult male tigers increase, we expect that only a few will be able to successfully defend female territories, while others will compete for access to females. Thus, we expect male tiger territories will be clustered around female territories and suitable habitat areas beyond female territories may go unused. Clustering of multiple males around female territories will increase the potential for intraspecific competition. Finally, to investigate the factors contributing to male-biased ASR in sites with limited connectivity, we also tested if male distribution was affected by inter-sex differences in movement probabilities (stemming from differences in dispersal behavior and habitat fragmentation). When adult survival is similar for both sexes, or when female survival > male survival -- male-biased ASR in populations can be an artifact of high rates of female emigration, and/or differential male immigration from surrounding populations (Smith 1993).

METHODS

Description of study area

Dudhwa Tiger Reserve (DTR) is located in the Terai-Duar savannas and grasslands ecoregion that spans areas of Nepal, India, Bhutan and Bangladesh (Olson et al., 1998; Fig. 3.1). DTR is comprised of Dudhwa National Park (~700 km^2), Katerniaghat Wildlife Sanctuary (WLS; ~450 km^2) and Kishanpur Wildlife Sanctuary (~200 km^2), established in 1977, 1975 and 1972 respectively. DTR's most productive wildlife habitats, grasslands and wetlands, comprise approximately 18 % of the overall area. Other habitats include dry deciduous Sal (*Shorea robusta*) forests, and mixed-dry deciduous forests and teak (*Tectonia grandis*) plantations. Within India, the last remnant patches of the once-extensive grassland-wetland mosaics that characterize the CTL are now restricted to small areas in and around DTR. DTR's management has undergone drastic changes over the past 150 years. Through the 19^{th} century and until about 1960, large forest tracts were exclusive hunting blocks for India's colonial administrators and Indian royalty. Other areas were intensively managed to supply high-grade Sal timber (Strahorn 2009).

The three PAs of DTR vary in their degree of connectedness with other tiger habitats in India and Nepal. Kishanpur Wildlife Sanctuary is embedded within a larger tiger habitat patch (~1400 km^2 Pilibhit forest complex in India) and connected with Shuklaphanta Wildlife Sanctuary in Nepal, via the Sharda River corridor. Katerniaghat WLS is connected to the 968 km^2 Bardia National Park via the 40 km long Khata corridor (along the Karnali River). Connectivity between Dudhwa National Park and Laljhari and Basanta community forests in Nepal has been severely compromised by land use change and expanding human settlements in recent decades (Kanagaraj et al. 2013; Chanchani et al. 2014a; Joshi et al. 2016). Finally, tiger density and ASR in DTR's

three PA's vary extensively. The highest tiger density (4.92 tigers/ 100 km^2) and most female-biased ASR (adult males = 29% of population) were recorded from Kishanpur WLS in 2013. In contrast, tiger densities were lower in Katerniaghat WLS (4.72 and 2.22 tigers/100 km2, (61% and 33% males in 2012 and 2013 respectively) and Dudhwa National Park (2013: 1.89 tigers/100 km2, 58% male) (Chanchani *et al*. 2014a; Jhala, Qureshi & Gopal 2016; Table 3.2, Table 3.3).

Camera Trap Sampling

Between November 2011 and June 2013, we conducted extensive camera-trap surveys to assess the status of tigers in the CTL. We used a grid-based sampling design and positioned pairs of cameras at intervals of approximately 2 km within tiger habitats. Pairs of camera traps were placed along forest trails or water courses to maximize detection probability. Camera trap surveys were completed in blocks of ≤ 60 days to meet the demographic closure assumption of capture recapture models (Karanth et al. 2002). At each location, cameras were operated from 14-56 days. Overall, 304 locations were sampled with camera traps from Novembe1r 2011- May 2012, and 380 locations were sampled from November - June 2013 (Table 3.2). Increased resources allowed us to sample a larger area in Katerniaghat WLS in 2013 than in 2012.

Data Processing, Model Formulation and Analysis

To evaluate our a priori hypotheses we fit multi state occupancy models to our camera trap data (Nichols et al. 2007). Camera trapping data have been traditionally analyzed in a mark-recapture framework to estimate demographic parameters (such as abundance and survival), but recent extensions of these methods allow estimates of patch occupancy and species co-occurrence (Nichols et al. 2007; O'Connell & Bailey 2011). Our study applies multi-state occupancy models to test hypotheses about spatial variability in tiger distribution and the influences of habitat connectivity and male-biased ASR on intraspecific behaviors.

Photo-captured adult tigers were individually identified from photos by three independent observers and by using pattern recognition software (Hiby et al., 2009). The sex of all tigers was discernible from the photos which allowed us to assign habitat-use states by sex and individual. We defined a sampling occasion as a 14 day period corresponding to the duration over which tiger spray scent (used for territorial marking) remains detectable (Smith et al. 1989). At each camera trap location and on every sampling occasion, male tiger captures were assigned to one of five habitat-use states. These states indicated probability of use of locations by single (ψ) or multiple (ψ') male tigers, in the presence/absence of females (*f*; Table 3.1). Tiger habitat use states were defined as: State 1, no male use (1- $\psi - \psi'$); State 2, location use by a single male and no female use ($\psi \times (1 - f)$); State 3, location use by single male, and female use ($\psi \times f$); State 4, use of location by multiple males and no female use ($\psi' \times (1 - f)$); and State 5, use by multiple males, and female use ($\psi' \times f$). Notations in parentheses are mathematical probability statements uniquely identifying each state. Multi-state occupancy models allow for state uncertainty. We accounted for non-detection of tigers by estimating misclassification probabilities – for example, we might observe a male tiger during a 14-day occasion (observe state 2) even though females were also present (true state 3); the probability of this misclassification is p_3_2 (Figure 2).We estimated model parameters using a hierarchical Bayesian multi-state occupancy model (Royle & Dorazio 2008; Kery & Schaub 2012). The true (latent) state of each location (trap station), *z*, can take on state values equal to 1, 2, 3, 4 or 5, corresponding to the five habitat use states. *z* is modeled by estimating Ω_i, the state vector describing the probability that site *i* is in one of the five states. The observation process describes how the true state *z* is linked with the observations, $y_{i,j}$, the observed states of tiger habitat use at site *i* and occasion *j*. The conditional relationship between y_{ij} and *z* is described by a categorical distribution with the θ_z, representing the observation matrix

(Fig.3.2). The elements of the observation matrix are the probabilities of observing tiger use in each of the five states. Diagonal elements are the probabilities of correct classification and off-diagonals elements are the probabilities of misclassification. The probabilities in each row of the observation matrix sum to 1. Detection probabilities were allowed to vary among survey occasions (2 week-long periods).

Because sex-specific fine-scale habitat use by tigers was unknown to us, we specified vague logit normal priors for ψ and ψ' (Fig 2). The parameter *f* was modeled using a beta distribution prior. We used Dirchlet priors to describe the distribution of elements within observation array rows($p_{,n\_k:} p_{1\_k}$, $p_{2\_k,}$ p_{3_k}, $p_{4\_k,}$ and p_{5k}), where *n* represents the true state of a site and *k* represents the observed state. The Dirchlet distribution satisfies the requirement that the elements of each row of the observation array sum to 1 (Kery & Schaub 2012; Hobbs & Hooten 2015). We fit our Bayesian model using Monte-Carlo-Markov Chain (MCMC) algorithms implemented in program JAGS (Plummer 2003) linked to program R (R Development Core Team). We separately analyzed data for three PA's in DTR in each of the two survey years. The analysis for each data-set included three chains, each with 100,000 MCMC iterations, and a burn-in value of 10,000.

Model Support and Evaluation

To assess departures from similarity for posterior distributions of estimated parameters and model support, we used a one-sided test based on Bayesian *p* values. Specifically, to test whether a given prediction was supported—for example, that probability of multiple-male tigers using a location would be higher at sites with male-biased ASR $(\psi'_{site\ 2} \times f_{site2})$ than in sites with female-biased ASR $(\psi'_{site\ 1} \times f_{site1})$—we computed:

$\sum_{i=1}^{n.mcmc}((\psi'_{site2} \times f_{site2}) - (\psi'_{site1} \times f_{site1}))>0/\ n.mcmc,$

where *N.mcmc* is the number of MCMC iterations. If the posterior distributions were exactly the same, we expect a value of 0.5 (i.e., given any value from $(\psi' \times (f))_{site2}$ compared to $(\psi' \times (f))_{site1}$, 50% will be greater). Values >0.5 indicate support for the hypothesis. In a scenario where all samples in $(\psi' \times (f))_{site2} > (\psi' \times (f))_{site1}$, we expected a Bayesian *p* value of 1.

We assessed model fit via a posterior predictive check where simulated data sets for each site/year are compared with the original data sets (Gelman & Hill 2007). Further, we assessed whether the probabilities of the observed data were more extreme relative to the simulated data.

Estimating Survival of Adult Male and Female Tigers

We used Cormack-Jolly-Seber (CJS) models to estimate apparent annual survival rates for adult tigers (Lebreton et al. 1992). We refer to 'apparent' survival because mortality cannot be discriminated from permanent emigration and survival for at least one year (Karanth et al. 2006). Our estimates of survival were based on a four year (2010-2014) capture-recapture data set. To assemble capture histories for open population models, we used data from two separate sources. Data for 2012 and 2013 came from our camera trap studies. For the years 2010 and 2014, we identified individual tigers from published photo databases of individual tigers captured in DTR (Jhala et al. 2011, 2016). We separately estimated probabilities of apparent survival (Φ) and recapture probabilities (*p*) for the three PA's allowing for Φ and *p* to be constant, vary by sex or year, or both.

RESULTS

Over the two-year study period, with a cumulative sampling effort of 18,643 trap-nights, we photo-captured 62 unique adult tigers (>2 years in age). Of these, 29 (47%) were female and 33 (53%) male (Table 3.2). We were unable to estimate posterior parameters for Dudhwa National Park in 2012 because a large numbers of locations only had one sampling occasion (14 days). The relative proportions of tiger records in each of the five states varied across our study sites (Table 3.3). We did not find support for the hypothesis that habitat use by male tigers would be similar in sites with and without male-biased ASR. The Bayesian *p* values indicate that large proportions of available habitat would not be used by male tigers in sites with male-biased ASR (State 1; (1-$\psi - \psi'$)). Median posterior probability estimates for habitat use by male tigers were 1.5 - 2 times higher in in Kishanpur, than in sites with male-biased ASR (Dudhwa and Katerniaghat), (Fig 3.3, Table 4). Our hypothesis of low probability of habitat use by a single male tiger, given female presen3.ce (State 3; ($\psi \times f$)) in sites with male-biased/ even ASR, was generally supported. Model estimates also indicated support for one of our hypotheses about increased potential for intra-specific completion in sites with male-biased/ even ASR. Median estimates of the probability of habitat use by multiple male tigers and no use by female tigers (State 4; ($\psi' \times (1-f)$) were 1.5-2 times higher in sites with male-biased/ even ASR, than in Kishanpur, a site with a female-biased ASR. We note that ASR was male-biased in Katerniaghat WLS in 2012 but female-biased in 2013. We found less evidence in favor of our other hypothesis about increased potential for intraspecific completion in sites with male-biased ASR. Probabilities of fine-scale habitat use by multiple male tigers and females (State 5 ($\psi' \times (f)$)), appeared to be similar across sites, regardless of ASR, suggesting that dominant males may be highly effective in warding off territorial intrusions by

rivals. Finally, we also failed to find support for our hypothesis that the probability of fine-scale habitat use by male tigers and no females, would be higher in male-biased ASR sites than female-biased ASR sites (State 2 ($\psi \times (1\text{-}f)$). Instead, we found that probabilities were similar in the two site-categories.

Posterior predictive checks revealed no evidence of lack of fit because test statistics based on the observed data were not more extreme than test statistics calculated from the simulated data (Appendix 3.1).

Survival Estimates

Consistent with our hypotheses, there was no evidence that male-biased sex ratios were an artefact of differential survival of adult male and female tigers. Estimates of male and female survival were very similar in two of our three study sites (differences not statistically significant) (Fig. 4). Point estimates of female survival was highest in Kishanpur WLS (Φ=0.85, SE=0.06) and lower in our two other study sites with lower habitat connectivity. Estimates of male survival were similar in all three sites (Φ=0.65). Other than in Kishanpur WLS, models with sex-specific differences in survival were weakly supported relative to other models that assumed uniform survival probabilities for males and females. (Appendix 3.2).

DISCUSSION

Our study highlights some direct and indirect linkages between landscape fragmentation, variation in adult sex ratios, and demography of large carnivore populations. We show that habitat fragmentation may indirectly influence adult sex ratios in populations and potentially exacerbate the potential for intraspecific (both inter and intra-sex) competition in populations of territorial

species. While habitat fragmentation has previously been associated with population declines and loss of genetic heterozygosity (Mondol, et al. 2013), the 'indirect' impacts of fragmentation on population demography and individual fitness have received less attention, even though is recognize that the omission of spatial structure can undermine analysis of population vulnerability (Gilpin 1987).

Our study provides evidence that tiger space-use in a given habitat patch (site) is related to adult sex ratios which may arise from pronounced intra-specific aggression among males for access to females. In this context, three key findings in our study are relevant: (i) a large proportion of available habitat may go unused by tigers in sites with male-biased ASR, especially when populations are small; (ii) male tigers in sites with male-biased ASR may compete intensely for access to female territories; and (iii) intensified competition between males may have deleterious effects on survival of males, females and juveniles. We hypothesize that ratio of adult male: female tigers, in addition to the area of suitable habitat, may limit growth rates of some small tiger population. Results from Dudhwa National Park support this hypothesis. Over our study period, we recorded no tiger use in approximately 50% of the park including extensive grassland habitats that supported high tiger densities until approximately a decade ago (Jhala et al., 2008). Based on indirect evidence, we believe that female tigers may have been poached from these areas and not yet recolonized by females. The distribution of capture histories across male tigers suggests the existence of a dominance hierarchy among Dudhwa's adult male tigers. In 2013, two of seven adult males in the population contributed 68.2% of all male tiger detections from camera traps. Space-use by these two males extensively overlapped the presumed territories of 4 of 7 females. Past studies have documented that prey availability, habitat characteristics and human disturbance explained spatial heterogeneity in tiger distributions (Karanth et al. 2011; Harihar & Pandav 2012;

Chanchani et al. 2016). When these covariates have weak explanatory power (or relationships are associated with high uncertainty), tiger distributions may be more strongly driven by skewed sex ratios, poaching (particularly the loss of females), and habitat fragmentation and isolation.

Skewed adult sex ratios may have local effects on demography and population structure. Models of equilibrium occupancy for territorial species predict that mate finding difficulties may lead to Allee effects (Stephens et al. 1999). For tigers, we are referring specifically to depensation—a decrease in the size of the breeding population leading to reduced reproduction and lower population growth rates (Lande 1987). We believe small tiger populations in the Dudhwa National Park and Katerniaghat Wildlife Sanctuary may exist below the ecological carrying capacity of these sites as a consequence of a skewed ASR. Small, declining populations in recent decades may have been accelerated by poor recruitment, survival and low immigration of individuals, a result of poaching, habitat fragmentation and intraspecific competition (Barlow et al. 2009; Carter et al. 2015). Further, because the patches of riparian and tall grasslands that support high prey densities are now greatly reduced in area and subject to high human use, extant habitats may only support small tiger populations with high rates of patch -level extinction (Noon & McKelvey 1996). Estimated apparent survival probabilities for adult male and female tigers were ~ 10-15% lower in fragmented sites with male-biased ASR (Dudhwa and Katerniaght) relative to larger and better connected habitats including Nagarhole in Southern India and Huai Kha Khaeng Sanctuary in Thailand (Karanth et al. 2006; Duangchantrasiri et al. 2016). Chapron et al (2008) suggest that tiger populations with low adult survival (e.g., Katerniaghat and Dudhwa) remain extinction-prone even if significant measures are implemented too increase prey abundance.

We attribute small population sizes and low survival rates primarily to poaching, in part, a consequence of the proximity of our sites to the international border with Nepal. However, when

poaching is combined with skewed, male-biased ASR, the increased intraspecific competition and Allee effects have a synergistic negative effect on the populations (Lande 1998; Stephens & Sutherland 1999). In the CTL, we predict that male-biased ASR may result in reduced probabilities of encountering mates may be a consequence of both low population density and increased competition among males to gain access to females (Rankin et al. 2011; Wadekind 2012). Difficulty in encountering potential mates may be compounded by the occasional emigration of female tigers from protected areas. We documented two female tigers raising cubs in sugarcane plantations away from primary habitats in PAs and Reserve Forests. Such local movements, whether temporary or permanent, may be a response to the likelihood of infanticide from a novel, but dominant male (Ebensperger 1998; Swenson 2003; Singh et al. 2014). Further mortality of sub-dominant (and often younger males) that arise from territorial conflicts with established, dominant males may result in high rates of male mortality. One study in Nepal ascribed 50% of mortality of young male tigers to intra-sexual aggression (Smith 1993), even though the ASR in Chitwan National Park (Nepal) was ~ 1:3.

Finally, we note that overlapping space use by tigers, as inferred from camera trap data, is an indirect measure of the potential for intra-specific conflict and does not provide probabilities or frequencies of occurrence of actual conflict. Further, our results highlight that variation in ASR are temporally dynamic, and that skewed ASR may be reversed by B-I-D-E processes. In our study, we recorded transtions in ASR from male-biased to female-biased in one site, Katerniaghat WLS. Such switches may be triggered by sex biased mortality or immigration/ emigration of a few individuals from or into small populations. We speculate that such reversals in ASR may more likely be observed in sites with good habitat connectivity, than those with poor connectivity.

Conservation and Management Implications

The maintenance of viable tiger metapopulations in the CTL requires that structural habitat connectivity be maintained and that all available habitats, regardless of PA designation, be effectively protected (Chanchani et al. 2016) In many areas of the CTL, the lack of effective protection from poaching has led to large habitat tracts that support very low tiger densities. For example, extensive tracts of suitable habitat in Nepal, only 1-2 kilometers away from the northern boundary of DNP, face inordinately high hunting pressure of both tigers and their prey. As a result, they rarely sustain breeding females whose offspring may disperse into Dudhwa NP's productive riparian habitats. However, our finding of male-biased ASR in DNP, despite lower male survival rates of resident males, suggests that males may occasionally immigrate into the Park from surrounding areas, potentially through the human dominated matrix. However, rapid land use change is severely degrading wildlife corridors around in the Terai, and may severely limit the movement of large mammals through the matrix (Joshi et al. 2016), Unfortunately the maintenance and restoration of vital wildlife corridors often have little political support, especially if they involve land acquisition or displacement of people. In the absence of formal corridors, we are increasingly documenting the use of the surrounding agricultural matrix by large carnivores (Athreya et al. 2013; Joshi et al. 2013). If policies can be developed to minimize human-wildlife conflict and increase human tolerance of tigers (and prey) in the agricultural matrix, it may be possible to compensate to some extent for inadequate amount of protected area and lack of law enforcement (Gosling 2003). Our study suggests that in the CTL there may be less than the assumed three adult females per male in many tiger populations, even in areas with good habitat connectivity. Similar skews in sex ratios may also exist among other large carnivore species (Palomares et al. 2012). The persistence of small tiger populations requires protecting and

increasing prey populations and maintaining high adult survival rates (Karanth & Stith 1999; Chapron et al. 2008). The success of these and other conservation measures requires not only upon political will, but also societal involvement in, and support for conservation (Rastogi et al. 2012; Oldekop et al. 2015). Finally, our study underscores that poaching and habitat fragmentation often result in male-biased ASR with the potential to accelerate rates of population decline. Managers must therefore focus on the timely implementation of mitigation measures such as the introduction of females into male-biased populations, in association with effective law enforcement, to facilitate population recovery and the persistence of large carnivores in human dominated landscapes (Lambertucci et al. 2013; Reddy et al. 2016).

TABLES

Table 3.1. Five occupancy states for male tigers and associated patterns of habitat-use. Male tigers are dark gray, females light gray. Images of two tigers together imply site use by multiple male tigers. Shaded bars represent gradients of habitat connectivity, adult sex ratio and expected estimates of apparent survival.

Occupancy state for male tigers		Probability of fine-scale habitat use by male tigers		Specific hypotheses
		Category 1	Category 2	
State 1 (1-Ψ-Ψ')	No male use	High (+ +)	Low (- -)	High probability that large areas of available habitat may go unused by male tigers in sites with male-biased ASR, because males hone in on female territories.
State 2 Ψ(1-f)	Use by single male tiger and no female use	High (+)	Low (-)	A few dominant males are expected to secure and restrict access to females in sites with male- biased ASR. Thus, higher likelihood of male tiger use outside of female territories is expected.
State 3 Ψ(f)	Use by multiple male tigers and female use	Low (-)	High (+)	In sites with male-biased ASR, a few dominant males will secure and restrict access to females. In sites with female-biased ASR, there is a higher probability that every male tiger in the population will have access to one or more female(s).

State 4 Ψ'(1-f)	Use by multiple male tigers and no female use	High (+ +)	Low (-)	High probability of shared habitat use by multiple male tigers in sites with male-biased ASR because of increased intraspecific competition for mates. Shared use of sites expected in the vicinity of female home-range boundaries.
State 5 Ψ'(f)		High (+)	Low (-)	High probability of shared habitat use by multiple male tigers in sites with male-biased ASR because of increased intraspecific competition for mates. Territorial behavior may reduce shared use of locations, relative to sites with no female use.

Footnotes:

Category 1 sites (e.g. Dudhwa National Park) have the following characteristics:
- Poor habitat connectivity
- Male-biased/ even ASR
- Lower adult survival rates (expected)

Category 2 sites (e.g. Kishanpur Wildlife Sanctuary) have the following characteristics:
- Good habitat connectivity
- Female-biased ASR
- Higher adult survival rates.

Table 3.2. Details of camera trap effort in DTR's three protected areas. p_{mix} is the estimated proportion of males in the population based on a spatially-explicit, capture-recapture model. DNP and Katerniaghat have male-biased/even sex ratios and relatively poor habitat connectivity. Kishanpur has female-biased sex ratios and good habitat connectivity.

Site	Year	No. of Cameras	Effort (trap nights)	M_t+1	Total captures	No. of females	No. of female captures	No. of males	No. of male captures	p_{mix}*
DNP	2012	159	2626	14	126	5	42	9	84	0.58
DNP	2013	202	4861	14	274	7	92	7	182	0.47
Katerniaghat	2012	82	2190	18	88	7	35	11	53	0.61
Katerniaghat	2013	111	3663	17	207	11	106	7	101	0.33
Kishanpur	2012	63	2648	16	264	11	119	8	145	0.29
Kishanpur	2013	67	2655	15	254	9	151	6	103	0.4
TOTALS		**684**	**18643**	**94**	**1213**	**50**	**545**	**48**	**668**	

Table 3.3. Estimated tiger density, details of habitat connectivity and proportions of captures in each state for sites sampled with camera traps in the study area. Tiger habitat use states were: State 1 no male use; State 2, location use by a single male and no female use; State 3, location use by single male, given female use; State 4, use of location by multiple males given no female use; and State 5, use by multiple males, given female use.

Site	Year	Estimated tiger density/100 km2	ASR (p_{mix})	Habitat connectivity status
DNP	2012	2.05 (0.38)	0.58	Tenuous connectivity with multiple use forests in Nepal via Laljhari and Basanta corridors.
DNP	2013	1.89 (0.34)	0.47	
Katerniaghat	2012	4.72 (0.92)	0.61	Connectivity with Bardia National Park in Nepal, via Khata corridor.
Katerniaghat	2013	2.22 (0.40)	0.33	
Kishanpur	2012	5.45 (1.29)	0.29	Contiguous with Pilibhit and South Kheri forest divisions, and connected with Shuklaphanta WLS in Nepal via Sharda river corridor.
Kishanpur	2013	4.92 (0.88)	0.40	

Table 3.4. Bayesian *p* values to test hypotheses about differences in fine scale occupancy of tigers across gradients of adult sex ratios and habitat connectivity. When distributions were exactly the same, the Bayesian p values would be 0.5. Values >0.5 would indicate that our hypothesis (indicated by > sign) was supported. Values <0.5 signified the opposite.

		Hypothesis about occupancy & Bayesian *p* values		
Year	State	DNP>KPUR (MBI>FBC)	KGHAT>KPUR (MBSC>FBC)	DNP>KGHAT (MBI>MBSC)
2012	1 (1-Ψ- Ψ')		0.99	
2013	1 (1-Ψ- Ψ')	0.95	1	0.03
2012	2 Ψ (1-f)		0.45	
2013	2 Ψ (1-f)	0.31	0.21	0.55
2012	3 Ψ (f)		0.01	
2013	3 Ψ (f)	0.01	0.01	0.43
2012	4 Ψ' (1-f)		0.66	
2013	4 Ψ' (1-f)	0.97	0.79	0.92
2012	5 Ψ' (f)		0.28	
2013	5 Ψ' (f)	0.67	0.40	0.74

Footnotes: Dudhwa National Park (DNP) had even/ male-biased sex ratios and poor habitat connectivity. Kishanpur Wildlife Sanctuary (KPUR) had female-biased adult sex ratios and good habitat connectivity. Adult sex ratios in Katerniaghat Wildlife sanctuary (KGHAT) fluctuated between strongly male-biased and female-biased over the study period this site is connected to a PA in Nepal via a forest corridor. MBI - male-biased and isolated; FBC - female-biased and well connected; MBSC - male-biased, connected via a single corridor.

FIGURES

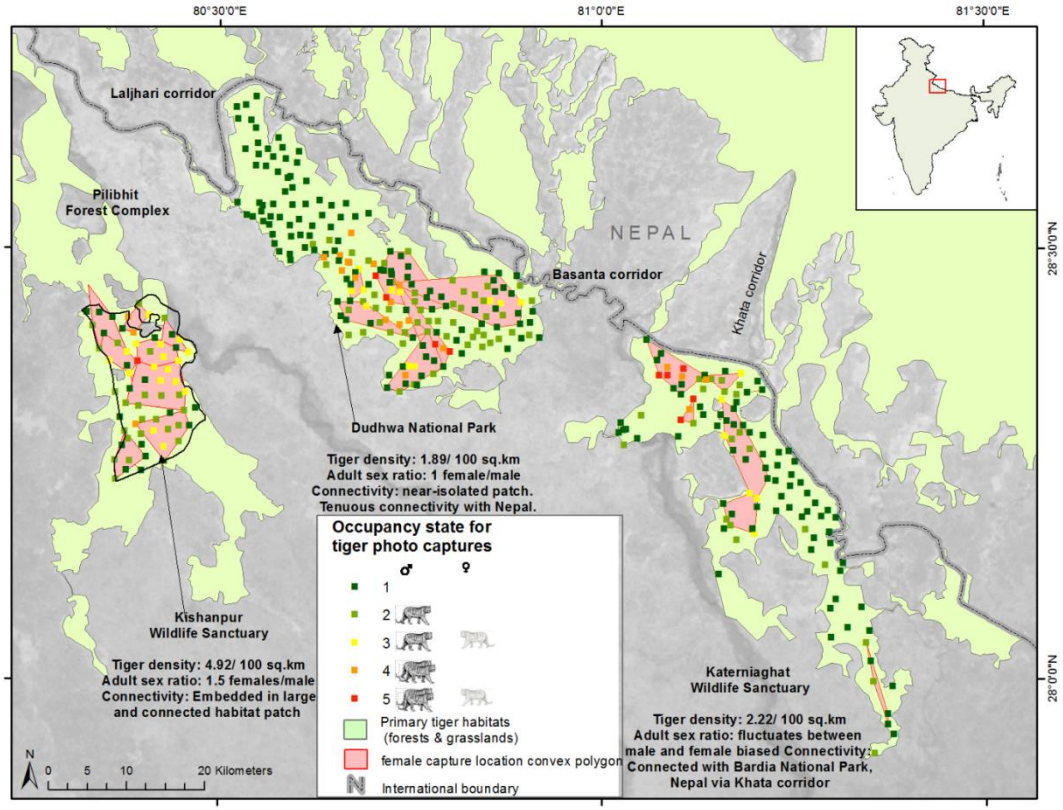

Figure 3.1. Map of the Central Terai Landscape depicting female home range locations, and state-wise ‘photo-capture locations of male tigers (in 2013). The approximate 'home ranges' of females tigers (defined by minimum convex polygons around capture locations) are delineated in beige.

Ecological Process: $z_i \sim Categorical(\Omega_i)$

$$\Omega_i = \begin{bmatrix} 1-\psi-\psi' \\ \psi \times (1-f) \\ \psi \times f \\ \psi' \times (1-f) \\ \psi' \times f \end{bmatrix} \begin{matrix} \text{State 1} \\ \text{State 2} \\ \text{State 3} \\ \text{State 4} \\ \text{State 5} \end{matrix}$$

Observation Process: $y_{i,j} | zi \sim Categorical(\theta[_{zi(S),j}])$

$$\theta_{z_{i,j}} = \begin{array}{c} \text{Observation state} \\ \begin{matrix} \text{State 1} & \text{State 2} & \text{State 3} & \text{State 4} & \text{State 5} \end{matrix} \end{array} \text{True state}$$

$$\begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 1-p_2 & p_2 & 0 & 0 & 0 \\ p_{3\_1} & p_{3\_2} & 1-p_{3\_1}-p_{3\_2} & 0 & 0 \\ p_{4\_1} & p_{4\_2} & 0 & 1-p_{4\_1}-p_{4\_2} & 0 \\ p_{5\_1} & p_{5\_2} & p_{5\_3} & p_{5\_4} & 1-\Sigma(p_{5\_1}, p_{5\_2}, p_{5\_3}, p_{5\_4}) \end{bmatrix} \begin{matrix} \text{State 1} \\ \text{State 2} \\ \text{State 3} \\ \text{State 4} \\ \text{State 5} \end{matrix}$$

Occupancy State Priors: $lpsi \sim Normal(0,100), \psi' \sim Normal\ (0,100), f \sim Beta(1,1)$

To constrain the parameters ψ *and* ψ' of the state matrix such that their sum is ≤ 1 , we used a logit transformation

$$\psi = \frac{e^{lpsi}}{1+e^{lpsi}+e^{lpsi1}}, \text{ and } \psi' = \frac{e^{lpsi1}}{1+e^{lpsi}+e^{lpsi1}}$$

Detection Priors: $p_2 \sim$ Beta(0,1),

parameters p_{3_1} through p_{5_5} are described by a Dirchlet distribution, described by the hyperprior random variable $\beta \sim$ Gamma(1,1), followed by $p_i = \beta_{i,t} / \sum_{i=1}^{5} \beta$

Joint Posterior Distribution:

$$[\Omega, \theta | y] \propto [yi | \Omega \times \theta]\ [\Omega | \psi, \psi', f]\ [\theta |\ p_2, p_{3\_1}, p_{3\_2}, p_{4\_1}, p_{4\_2}, p_{5\_1}, p_{5\_2}, p_{5\_3}, p_{5\_4}]\ [\psi]\ [\psi']\ [f]\ [p_2][p_{3\_1}][p_{3\_2}]$$
$$[p_{4\_1}][p_{4\_2}][p_{4\_3}][p_{4\_1}][p_{4\_2}][p_{5\_1}][p_{5\_2}][p_{5\_3}][p_{5\_4}]$$

Figure 3.2. Bayesian, multi state occupancy model used to test hypothesis about habitat use and intra-specific completion among male tigers. The five true (latent) habitat use states are State 1: no male use; State 2: location use by single male tiger and no female use;

State 3: habitat use by a single male tiger and female use; State 4: habitat use by multiple male tigers and no female use; State 5: habitat use by multiple male tigers, and female use. The observation matrix (θ) details the observation process associated the detection of tigers in each of the five habitat use states at site (i) and sampling occasion (j). The diagonal elements are the probabilities of correct classification and the all off-diagonals are probabilities of mis-classification of a state. The probabilities in each row of the matrix sum to 1. All p_{ij} are vectors of detection parameters that vary by time.

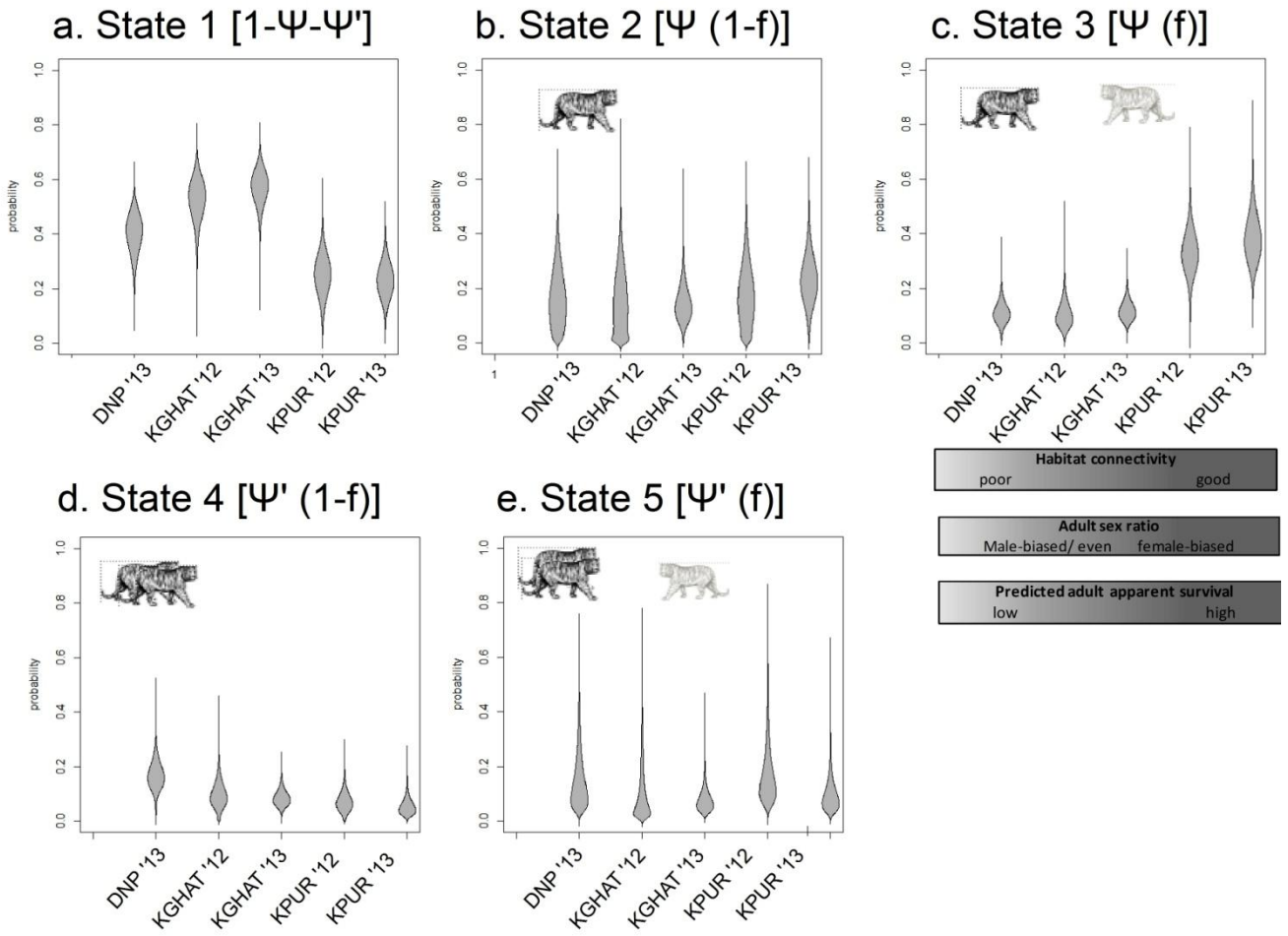

Figure 3.3: posterior distributions for parameters linked to the five habitat use states for three PAs in DTR (DNP: Dudhwa NP, KGHAT: Katerniaghat WLS and KPUR: Kishanpur WLS). These PAs span gradients of habitat connectivity and ASR (mal- biased to female-biased). The width of the strip in these plots is proportional to the density.

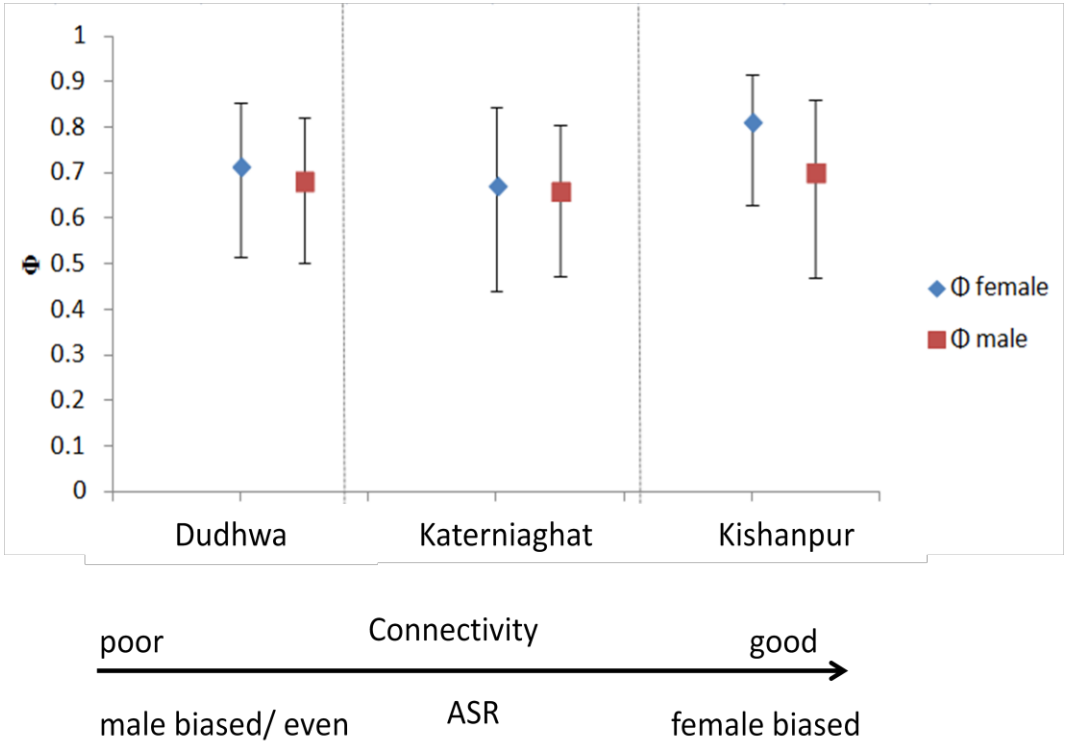

Figure 3.4. Model averaged estimates of apparent survival probability of male and female tigers in DTR's three protected areas over a 4-year period (2010-2014).

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Appendix 1.1. Description of the statistical model

We employed a modified version of the Hines et al., (2010) occupancy model that is suitable for spatially autocorelated species detection-non-detection data collected along linear features, such as trails. The Hines et al. (2010) model provides estimates of species occupancy at the scale of the primary sampling unit (cell), via a single survey of a series of trail segments with first order (Markov) spatial dependence. The model has four parameters: ψ, the probability that a unit (cell) is occupied, θ and θ', the conditional (on occupancy) probability that a segment is used given that the previous segment was or was not used, respectively, and *p*, the probability of detecting the species on a used segment. While this model addresses the potential lack of statistical independence arising from the detection of animal signs on adjacent trail segments, it cannot differentiate among factors influencing segment-level use and detection. Most applications of this model have simply assumed that parameters θ and θ' are constant across segments (e.g., Karanth et al. 2011, Sunarto et al. 2012, Linkie et al. 2015)

Our modification of the Hines et al. (2010) serves to disentangle local (segment-level) occupancy from detection by employing *k* replicate surveys of each segment. For example, a detection history, h_j for three successive trail segments, each surveyed k=2 times is 010011. Here, the first 0 implies that the species was not detected during the first survey (group of surveyors) of the first segment, but was detected during the second survey (by the second group of observers). The associated probability follows:

$$\Pr(h_j = 010011) = \psi(\theta(1-p_1)\, p_2)[(\theta'(1-p_1)(1-p_2)\, \theta'(\, p_1\, p_2)) + (1-\, \theta')\theta(\, p_1\, p_2)]$$

The subscripts p_1 and p_2 reference the replicate surveys (observer groups). The unit is clearly occupied (ψ) and the first segment is used by the species, but this use was only detected during

the second survey For segment 2, there are two possibilities -- the species could have used the segment (θ') but was not detected in either survey, or the species did not use the segment (1- θ'). The third segment was clearly used by the species because it was detected by both surveys, and the only source of uncertainty relates to whether or not the species also used the previous segment.

The likelihood associated with this model is:

$L(\psi,\theta,\theta',p|h_1, h_2, h_3 \ldots h_n) = \prod_{j=1}^{n} Pr(h_j)$

This 'robust-design' modification of the Hines et al (2010) model is available both in program PRESENCE and program MARK.

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Appendix 1.2. Modeling and selection strategy to evaluate the influence of PA, MUF, grassland and total habitat on tiger occupancy. Step 1: determining a global model structure.

A key objective of our study was to determine influence of habitat covariates (i.e. area encompassed by PA or MUF within a cell, total habitat area and grassland area) on tiger occupancy. Specifically, we had hypothesized that total habitat area or grassland area within a cell, rather than protection designation, would influence tiger occupancy.

In the first step of our analysis, we sought to determine one (or more) 'global' models with high support, which would then be carried forward to steps 2 and 3 of the analysis, where the objective was to ascertain covariate influence on detection probability (p) and fine scale habitat use (θ and θ'), respectively. *A priori*, we believed that a global model would include covariates that related to habitat, prey, human disturbance, etc. to tiger occupancy at either the cell scale and/or fine scale habitat use at the segment scale. Specifically, a global model would have the following structure: Ψ (hum-live + *habitat* + *prey* + hum-live * *habitat), θ & θ'* (understory + H_20 + d-ag +*habitat* + *prey* +hum-live), p (soil + tread). There were multiple candidate *habitat* and *prey* covariates, and we did not know *a-priori* which of these would be best supported. Hence, in the first analysis step, we use an information theoretic approach to (i) test hypotheses regarding PA, MUF and habitat attributes in a cell; and (ii) identify a global model.

Table A1 lists all 64 candidate global models. In any given model, we only consider one of the four *habitat* covariates (PA, MUF, total-area, or grass) for the ψ and θ parameters. Similarly we only consider one of the two alternate *prey* covariates (i.e., prey-ER or prey-high) for the ψ and θ parameters.

Table A2 is a list of model selection results for the aforementioned 64 possible global models, including model weights and deviance. Table A3 lists estimated coefficient values and standard errors for the covariates included in the models with $w>0$. Readers may find it helpful to refer to the column "Model #", which provides an easily interpretable link between Tables A1, A2 and A3. A list of covariates associated with models in Appendix S1 appears in the footnotes of Table A1.

Table A1.1. List of alternative global model structures to determine influence of habitat covariates (PA, MUF, TotalArea and Grassland Area) on broard and fine scale tiger occurrence.

Mod #	Covariates in global model structures for tiger occupancy (Ψ)	Covariates representing different combinations of *habitat and prey* for global model structures for fine scale tiger use, (θ & θ' (understory + H_20 + d-ag +*habitat* + *prey* +hum-live). The effects of understory (us), H_20, d-ag and hum-live are included in every model.		
		Protection designation/ habitat attribute	prey-high	prey-ER
1.1	PA + prey-high + hum-live + PA*hum-live	PA	x	
1.2	PA + prey-high + hum-live + PA*hum-live	MUF	x	
1.3	PA + prey-high + hum-live + PA*hum-live	total-area	x	
1.4	PA + prey-high + hum-live + PA*hum-live	grass	x	
1.5	PA + prey-high + hum-live + PA*hum-live	PA		x
1.6	PA + prey-high + hum-live + PA*hum-live	MUF		x
1.7	PA + prey-high + hum-live + PA*hum-live	total-area		x
1.8	PA + prey-high + hum-live + PA*hum-live	grass		x
2.1	PA + prey-ER + hum-live + PA*hum-live	PA	x	
2.2	PA + prey-ER + hum-live + PA*hum-live	MUF	x	
2.3	PA + prey-ER + hum-live + PA*hum-live	total-area	x	
2.4	PA + prey-ER + hum-live + PA*hum-live	grass	x	
2.5	PA + prey-ER + hum-live + PA*hum-live	PA		x
2.6	PA + prey-ER + hum-live + PA*hum-live	MUF		x
2.7	PA + prey-ER + hum-live + PA*hum-live	total-area		x
2.8	PA + prey-ER + hum-live + PA*hum-live	grass		x
3.1	MUF + Prey High + hum-live + MUF*hum-live	PA	x	
3.2	MUF + Prey High + hum-live + MUF*hum-live	MUF	x	
3.3	MUF + Prey High + hum-live + MUF*hum-live	total-area	x	
3.4	MUF + Prey High + hum-live + MUF*hum-live	grass	x	

	7.5	grass + Prey High + hum-live + grass*hum-live	PA		x
	3.6	MUF + Prey High + hum-live + MUF*hum-live	MUF		x
	3.7	MUF + Prey High + hum-live + MUF*hum-live	total-area		x
	3.8	MUF + Prey High + hum-live + MUF*hum-live	grass		x
	4.1	MUF + prey-ER + hum-live + MUF*hum-live	PA	x	
	4.2	MUF + prey-ER + hum-live + MUF*hum-live	MUF	x	
	4.3	MUF + prey-ER + hum-live + MUF*hum-live	total-area	x	
	4.4	MUF + prey-ER + hum-live + MUF*hum-live	grass	x	
	4.5	MUF + prey-ER + hum-live + MUF*hum-live	PA		x
	4.6	MUF + prey-ER + hum-live + MUF*hum-live	MUF		x
	4.7	MUF + prey-ER + hum-live + MUF*hum-live	total-area		x
	4.8	MUF + prey-ER + hum-live + MUF*hum-live	grass		x
	5.1	total-area + Prey High + hum-live + total-	PA	x	
	5.2	total-area + Prey High + hum-live + total-	MUF	x	
	5.3	total-area + Prey High + hum-live + total-	total-area	x	
	5.4	total-area + Prey High + hum-live + total-	grass	x	
	5.5	total-area + Prey High + hum-live + total-	PA		x
	5.6	total-area + Prey High + hum-live + total-	MUF		x
	5.7	total-area + Prey High + hum-live + total-	total-area		x
	5.8	total-area + Prey High + hum-live + total-	grass		x
	6.1	total-area + prey-ER + hum-live + total-	PA	x	
	6.2	total-area + prey-ER + hum-live + total-	MUF	x	
	6.3	total-area + prey-ER + hum-live + total-	total-area	x	
	6.4	total-area + prey-ER + hum-live + total-	grass	x	
	6.5	total-area + prey-ER + hum-live + total-	PA		x
	6.6	total-area + prey-ER + hum-live + total-	MUF		x
	6.7	total-area + prey-ER + hum-live + total-	total-area		x
	6.8	total-area + prey-ER + hum-live + total-	grass		x
	7.1	grass + Prey High + hum-live + grass*hum-live	PA	x	
	7.2	grass + Prey High + hum-live + grass*hum-live	MUF	x	
	7.3	grass + Prey High + hum-live + grass*hum-live	total-area	x	
	7.4	grass + Prey High + hum-live + grass*hum-live	grass		x

7.6	grass + Prey High + hum-live + grass*hum-live	MUF		x
7.7	grass + Prey High + hum-live + grass*hum-live	total-area		x
7.8	grass + Prey High + hum-live + grass*hum-live	grass	x	
8.1	grass + Prey ER + hum-live + grass*hum-live	PA	x	
8.2	grass + Prey ER + hum-live + grass*hum-live	MUF	x	
8.3	grass + Prey ER + hum-live + grass*hum-live	total-area	x	
8.4	grass + Prey ER + hum-live + grass*hum-live	grass	x	
8.5	grass + Prey ER + hum-live + grass*hum-live	PA		x
8.6	grass + Prey ER + hum-live + grass*hum-live	MUF		x
8.7	grass + Prey ER + hum-live + grass*hum-live	Habitat		x
8.8	grass + Prey ER + hum-live + grass*hum-live	grass		x

Footnotes:

Covariates: d-ag: prevalence of dwellings and agriculture along trail segments; H_2O: prevalence of water bodies along trail segments; understory: prevalence of grassy understory along trail segments; prey-ER: sum of encounter rates for prey signs (7 species) along 1 km segments within a cell; prey-high: sum of encounter rates for multiple prey signs (7 species) along 1 km trail segments within a cell; hum-live: sum of human and cattle encounter rates along 1 km trail segments within a cell; PA: extent of PA within a cell; MUF: extent of MUF within a cell; total-area: extent of primary tiger habitat (grasslands and forests, PA + MUF) within a cell; grass: extent of grasslands within a cell. For detailed information for covariates, see Table 1.

Table A1.2. Model selection results for Step 1, determining 'best' global model structure. The models test hypotheses for protection designation and habitat attributes (*habitat)* and *prey* covariates.

Model #	Model[a]	Δ AICc[b]	w^c	K^d	$-2l^e$
7.8	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	0.00	0.68	16	1600.08
7.4	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	3.09	0.14	16	1603.17
8.8	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	4.96	0.06	16	1605.04
5.8	ψ(prey-high+total-area*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	5.35	0.05	16	1605.43
7.7	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	6.97	0.02	16	1607.05
3.8	ψ(prey-high+MUF+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	7.55	0.02	16	1607.63
8.4	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	8.30	0.01	16	1608.38
5.4	ψ(prey-high+TotaArea+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	8.69	0.01	16	1608.77
1.8	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	9.96	0.00	16	1610.04
3.4	ψ(prey-high+MUF+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	10.57	0.00	16	1610.65
7.5	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	10.72	0.00	16	1610.80
8.7	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	10.80	0.00	16	1610.88
5.7	ψ(prey-high+total-area+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	12.24	0.00	16	1612.32

7.3	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-high+hum-live)	12.44	0.00	16	1612.52
1.4	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	13.13	0.00	16	1613.21
7.6	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	14.50	0.00	16	1614.58
3.7	ψ(prey-high+MUF+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	14.94	0.00	16	1615.02
6.4	ψ(prey-ER+total-area+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	15.31	0.00	16	1615.39
6.8	ψ(prey-ER+total-area+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	15.33	0.00	16	1615.41
7.1	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	15.45	0.00	16	1615.53
8.5	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	16.09	0.00	16	1616.17
8.3	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-high+hum-live)	16.69	0.00	16	1616.77
5.5	ψ(prey-high+total-area+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	17.59	0.00	16	1617.67
1.7	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	17.76	0.00	16	1617.84
5.3	ψ(prey-high+total-area+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-high+hum-live)	17.99	0.00	16	1618.07
7.2	ψ(prey-high + grass+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-high+hum-live)	18.98	0.00	16	1619.06
3.5	ψ(prey-high+MUF+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	19.25	0.00	16	1619.33
8.6	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	19.75	0.00	16	1619.83
6.7	ψ(prey-ER+total-area+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	20.09	0.00	16	1620.17
3.3	ψ(prey-high+MUF+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-	20.43	0.00	16	1620.51

	high+hum-live)				
8.1	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	21.15	0.00	16	1621.23
1.5	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	21.43	0.00	16	1621.51
5.6	ψ(prey-high+total-area+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	21.54	0.00	16	1621.62
6.3	ψ(prey-ER+total-area+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-high+hum-live)	22.27	0.00	16	1622.35
4.4	ψ(prey-ER+MUF+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	22.68	0.00	16	1622.76
5.1	ψ(prey-high+total-area+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	22.79	0.00	16	1622.87
2.8	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	22.89	0.00	16	1622.97
4.8	ψ(prey-ER+MUF+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-ER+hum-live)	23.00	0.00	16	1623.08
3.6	ψ(prey-high+MUF+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	23.14	0.00	16	1623.22
6.5	ψ(prey-ER+total-area+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	23.31	0.00	15	1627.13
1.3	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-high+hum-live)	23.89	0.00	16	1623.97
3.1	ψ(prey-high+MUF+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	24.09	0.00	16	1624.17
8.2	ψ(prey-ER + grass+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-high+hum-live)	24.48	0.00	16	1624.56
1.6	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	25.32	0.00	16	1625.40
2.4	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+grass+prey-high+hum-live)	25.69	0.00	16	1625.77
5.2	ψ(prey-high + total-area+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-high+hum-live)	26.30	0.00	16	1626.38

1.1	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	26.43	0.00	16	1626.51
6.6	ψ(prey-ER+total-area+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	27.49	0.00	15	1631.32
3.2	ψ(prey-high + MUF+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-high+hum-live)	27.57	0.00	16	1627.65
4.7	ψ(prey-ER+MUF+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	29.01	0.00	16	1629.09
1.2	ψ(prey-high+PA+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-high+hum-live)	29.90	0.00	16	1629.98
2.7	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-ER+hum-live)	30.52	0.00	16	1630.60
6.1	ψ(prey-ER+total-area+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	30.81	0.00	16	1630.89
4.3	ψ(prey-ER+MUF+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-high+hum-live)	33.50	0.00	16	1633.58
6.2	ψ(prey-ER + total-area+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-high+hum-live)	33.70	0.00	16	1633.78
2.5	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	35.94	0.00	16	1636.02
4.5	ψ(prey-ER+MUF+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-ER+hum-live)	36.30	0.00	16	1636.38
2.3	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+total-area+prey-high+hum-live)	37.34	0.00	16	1637.42
4.1	ψ(prey-ER+MUF+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	40.02	0.00	16	1640.10
2.6	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	40.09	0.00	16	1640.17
4.6	ψ(prey-ER+MUF+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-ER+hum-live)	40.14	0.00	16	1640.22
2.1	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+PA+prey-high+hum-live)	41.17	0.00	16	1641.25
4.2	ψ(prey-ER + MUF+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-	42.05	0.00	16	1642.13

	high+hum-live)				
2.2	ψ(prey-ER+PA+*hum-live) θ&θ'(d-ag+H2O+us+MUF+prey-high+hum-live)	44.34	0.00	16	1644.42

Footnotes:

a:*p* structure for all models is *p*(soil + tread), covariate descriptions available at end of Table A1 and in Table 1. We have used the notation "grass+*hum-live"to index interactive models, which can also be expressed as grass+hum-live + grass*hum-live.

b: ΔAIC_c is the difference in AIC_c between the best supported model and any given model.

c: *w* is the AIC_c model weight.

d: *K* is the number of parameters

e: -2*l* is twice the negative log likelihood.

Table A1.3. Coefficient values and standard errors (in parentheses) for candidate global models with *w*>0. For detailed descriptions of covariates, refer to Table 1.

		Coefficient values for protection designation/ habitat attribute covariates associated with tiger occupancy (ψ)						Coefficient values for protection designation/ habitat attribute covariates associated with θ and θ' parameters			
Model #	Model	Prey ER	prey-high	grass	total-area	PA	MUF	prey-ER	prey-high	grass	total-area
7.8	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+understory+grass+prey-ER+hum-live)		7.53 (3.79)	-0.07 (0.31)				0.38 (0.18)		0.03 (0.01)	
7.4	ψ(prey-high+grass+*hum-live) θ&θ'(d-ag+H2O+understory+grass+prey-high+hum-live)		7.57 (4.06)	-0.05 (0.20)					0.26 (0.23)	0.03 (0.01)	
8.8	ψ(prey-ER+grass+*hum-live) θ&θ'(d-ag+H2O+understory+grass+prey-ER+hum-live)	-1.21 (0.82)		0.02 (0.12)				0.41 (0.18)		0.03 (0.01)	
5.8	ψ(prey-high+total-area+*hum-live) θ&θ'(d-ag+H2O+understory+grass+prey-ER+hum-live)		9.22 (4.00)		0.03 (0.02)			0.40 (0.18)		0.03 (0.01)	

	ψ(prey-high+grass+*hum-live) θ&θ'(d-								0.01 (0.002)
7.7	ag+H2O+understory+Hab+prey -ER+hum-live)		7.61 (4.05)	-0.06 (0.17)		0.57 (0.18)			
8.4	ψ(prey-ER+grass+*hum-live) θ&θ'(d- ag+H2O+understory+grass+pre y-high+hum-live)	-0.94 (0.82)		0.02 (0.15)			0.31 (0.23)	0.03 (0.01)	
5.4	ψ(prey-high+total-area+*hum- live) θ&θ'(d- ag+H2O+understory+grass+pre y-high+hum-live)		8.92 (4.09)		0.03 (0.03)		0.29 (0.23)	0.03 (0.01)	

Appendix 1.3. Model building and selection strategy for tiger detection probability (*p*), the probability of detecting signs in a used segment.

We evaluated eight alternative models to determine the influence of visibility of tracks on different soil substratum (soil) and intensity of vehicle tracks (tread) on detection probability (*p*). We also included models where detection probability was constant among all used segments, denoted *p*(.). We incorporated uncertainty about the *prey* covariates for the fine scale habitat use (θ and θ') by considering two alternative structures: θ & θ' (d-ag + H_2O + understory + grass + prey-ER + hum-live) and (d-ag + H_2O + understory + grass + prey-high + hum-live). ΔAICc scores and model weights (*w*) were used to select a highly supported model structure (see Table A4), which was carried forward into subsequent analysis steps.

Table A1.4. Model selection results for detection probability models. Coefficient (β) and standard error estimates are also reported.

Model[a]	Δ AICc[d]	w^e	K	$-2l^f$	Estimated β (SE) soil	Estimated β (SE) tread
θ&θ' (d-ag + H2O + understory + grass + prey-ER + Humlive), p(Soil[b] + Tread[c])	1644.73	0.41	16	1600.08	-0.16(0.07)	-0.09(0.03)
θ&θ' (d-ag + H2O + understory + grass + prey-ER + Humlive), p(tread)	1645.99	0.22	15	1605.08		-0.08(0.03)
θ&θ' (d-ag + H2O + understory + grass + prey-ER + Humlive), p(soil)	1647.63	0.10	15	1606.72	-0.14(0.07)	
θ&θ' (d-ag + H2O + understory + grass + prey-ER + Humlive), p(.)	1647.81	0.09	14	1610.47		
θ&θ' (d-ag + H2O + understory + grass + prey-high + Humlive), p(soil + tread)	1647.82	0.09	16	1603.17	-0.16(0.07)	-0.08(0.03)
θ&θ' (d-ag + H2O + understory + grass + prey-high + Humlive), p(tread)	1649.04	0.05	15	1608.12		-0.07 (0.03)
θ&θ' (d-ag + H2O + understory + grass + prey-high + Humlive), p(soil)	1650.46	0.02	15	1609.54	-0.14 (0.07)	
θ&θ' (d-ag + H2O + understory + grass + prey-high + Humlive), p(.)	1650.66	0.02	14	1613.32		

Footnotes:

a: ψ structure for all models is: ψ((prey-high + grass + hum-live + grass * hum-live)

b: Index of the visibility of animal tracks.

c:Index of the intensity of vehicle signs.

d: ΔAIC_c is the difference in AIC_c between the best supported model and any given model.

e: *w* is the AIC_c model weight.

f: *K* is the number of parameters

g: -2*l* is twice the negative log likelihood

Appendix 1.4. Modeling building and selection strategy for fine scale habitat use (θ and θ') by tigers

We evaluated the influence of segment scale covariates -- water bodies (H_2O), human development (d-ag), grassy understory (us), and select cell scale covariates -- grass, prey-high, prey-ER, and hum-live on fine scale tiger habitat use (θ and θ'). Given that a cell is occupied, θ is the probability that a one kilometer long trail segment was used by tigers, given that the previous segment was not used. θ' is the probability of segment use, given that the previous segment was used. The difference in θ and θ' was modeled as an additive effect.

To model file scale habitat use by tigers, we built 96 models (Table A5). The following model structure for the parameters Ψ and *p* was used in conjunction with all models: Ψ(grass + Prey High + hum-live + grass * hum-live), θ & θ (…) *p*(soil + tread)**,** based on steps 1 and 2 of our analyses (see Tables A1 and A2). Detailed results for this analysis step are in Table A6.

Table A1.5 Structure for the candidate model set for estimating fine scale habitat use (θ and θ') by tigers. The occupancy structure ψ(prey-high + grass + hum-live + grass*hum-live) and detection probability structure *p*(soil+tread) were used for all models, based on the results from previous analyses.

	segment scale			cell scale covariates		
Model #[a]	**d-ag[b]**	**H_2O[c]**	**understory[d]**	**Grass[e]**	**prey-ER[f] OR prey-high[g]**	**hum**
1	(.)	(.)	(.)	(.)	(.)	(.)
2	x					
3		x				
4			x			
5	x	x	x			
6	x		x			
7	x	x				
8		x	x			
9	x			x		
10		x		x		
11			x	x		
12a&b	x				x	
13a&b		x			x	
14a&b			x		x	
15	x					x
16		x				x
17			x			x
18a&b	x			x	x	
19a&b		x		x	x	
20a&b			x	x	x	
21a&b	x				x	x
22a&b		x			x	x
23a&b			x		x	x
24	x			x		x
25		x		x		x
26			x	x		x
27a&b	x			x	x	x
28a&b		x		x	x	x
29a&b			x	x	x	x
30	x	x		x		
31a&b	x	x			x	
32	x	x				x
33a&b	x	x		x	x	
34a&b	x	x			x	x

35	x	x		x		x
36a&b	x	x		x	x	x
37		x	x	x		
38a&b		x	x		x	
39		x	x			x
40a&b		x	x	x	x	
41		x	x	x		x
42a&b		x	x		x	x
43a&b		x	x	x	x	x
44	x		x	x		
45a&b	x		x		x	
46	x		x			x
47a&b	x		x	x	x	
48a&b	x		x		x	x
49	x		x	x		x
50a&b	x		x	x	x	x
51	x	x	x	x		
52a&b	x	x	x		x	
53	x	x	x			x
54a&b	x	x	x	x	x	
55a&b	x	x	x		x	x
56	x	x	x	x		x
57a&b	x	x	x	x	x	x
58				x		
59a&b					x	
60						x
61a&b				x	x	
62a&b					x	x
63				x		x
64a&b				x	x	x

Footnotes:

a: Models indexed by an "a&b" have two alternate versions, one includes the covariate prey-ER and the other prey-high.

b: d-ag: Prevalence of dwellings and agriculture along trail segments.

c: H_2O: Prevalence of water bodies along trail segments.

d: understory: prevalence of grassy understory along trail segments.

e: Grassland area in cell.

f. Sum of encounter rates for prey signs (7 species) along 1 km segments within a cell

g. Sum of encounter rates for multiple prey signs (7 species) along 1 km trail segments within a cell.

h. Sum of human and cattle encounter rates along 1 km trail segments within a cell.

Table A1.6. Model selection results for the influence of covariates on fine scale tiger use of previously used (θ') and unused segments (θ); the difference was modeled as an additive effect. Estimated coefficients (β) and standard errors are given for models with w>0. The occupancy structure used for all models was: ψ(prey-high + grass + hum-live + grass * hum-live). The detection probability structure for all models was p (soil + tread).

Model[a,b]					Estimated β (SE)						
	Δ AIC[c]	w^d	K^e	$-2l^f$	d-ag	H2O	understory	grass	prey-ER	prey-high	hum-live
28 - θ & θ'(H**2**O + grass + prey-ER + hum-live)	0.00	0.35	14	1601.38		0.14 (0.05)		0.03 (0.01)	0.43 (0.17)		-0.04 (0.01)
36 - θ & θ'(d-ag + H2O + grass + prey-ER + hum-live)	2.83	0.09	15	1600.64	-0.09 (0.10)	0.13 (0.05)		0.03 (0.01)	0.40 (0.17)		-0.03 (0.01)
25 - θ & θ'(H2O + grass + hum-live)	2.84	0.09	13	1607.64		0.12 (0.05)		0.03 (0.01)			-0.05 (0.01)
43 - θ & θ'(H2O + understory + grass + prey-ER + hum-live)	2.97	0.08	15	1600.77		0.13 (0.05)	0.04 (0.05)	0.03 (0.01)	0.41 (0.18)		-0.03 (0.01)
28b θ & θ'(H2O + grass + prey-high + hum-live)	4.26	0.04	14	1605.64		0.11 (0.05)		0.03 (0.01)		0.32 (0.22)	-0.04 (0.01)
64 - θ & θ'(grass + prey-ER + hum-live)	4.33	0.04	13	1609.13				0.03 (0.01)	0.37 (0.17)		-0.03 (0.01)
35 - θ & θ'(d-ag + H2O + grass + hum-live)	4.45	0.04	14	1605.83	-0.13 (0.10)	0.11 (0.05)		0.03 (0.01)			-0.05 (0.01)
41 - θ & θ'(H2O + understory + grass + hum-live)	4.66	0.03	14	1606.04		0.11 (0.05)	0.06 (0.05)	0.03 (0.01)			-0.05 (0.01)
19 - θ & θ'(H2O + grass + prey-ER)	5.03	0.03	13	1609.83		0.11 (0.05)		0.02 (0.01)	0.70 (0.15)		
63 - θ & θ'(grass + hum-live)	5.78	0.02	12	1613.86				0.03 (0.01)			-0.05 (0.01)
57 - θ & θ'(d-ag + H2O + understory +	6.02	0.0	16	1600.	-0.09	0.13		0.03	0.38		-0.04

grass + prey-ER + hum-live)		2		08	(0.10)	(0.05)		(0.01)	(0.18)		(0.01)
64b θ & θ'(grass + prey-high + hum-live)	6.13	0.02	13	1610.93				0.03 (0.01)		0.38 (0.22)	-0.04 (0.01)
27 - θ & θ'(d-ag + grass + prey-ER + hum-live)	6.29	0.02	14	1607.67	-0.12 (0.10)			0.03 (0.01)	0.33 (01.7)		-0.03 (0.01)
36b θ & θ'(d-ag + H2O + grass + prey-high + hum-live)	6.36	0.01	15	1604.16	-0.12 (0.10)	0.11 (0.05)		0.03 (0.01)	0.29 (0.23)		-0.04 (0.01)
24 - θ & θ'(d-ag + grass + hum-live)	6.48	0.01	13	1611.28	-0.16 (0.10)			0.03 (0.01)			-0.04 (0.01)
29 - θ & θ'(understory + grass + prey-ER + hum-live)	6.56	0.01	14	1607.94			0.05 (0.05)	0.02 (0.01)	0.34 (0.17)		-0.03 (0.01)
56 - θ & θ'(d-ag + H2O + understory + grass + hum-live)	6.67	0.01	15	1604.48	-0.12 (0.10)	0.12 (0.05)	0.05 (0.05)	0.03 (0.01)			-0.05 (0.01)
43b θ & θ'(H2O + understory + grass + prey-high + hum-live)	6.68	0.01	15	1604.48		0.11 (0.05)	0.05 (0.05)	0.03 (0.01)		0.28 (0.23)	-0.05 (0.01)
26 - θ & θ'(understory + grass + hum-live)	6.88	0.01	13	1611.68			0.07 (0.05)	0.03 (0.01)			-0.04 (0.01)
27b θ & θ'(d-ag + grass + prey-high + hum-live)	7.53	0.01	14	1608.91	-0.14 (0.10)			0.03 (0.01)		0.34 (0.22)	-0.04 (0.01)
61 - θ & θ'(grass + prey-ER)	7.66	0.01	12	1615.74				0.02 (0.01)	0.61 (0.14)		
33 - θ & θ'(d-ag + H2O + grass + prey-ER)	7.74	0.01	14	1609.12	-0.08 (0.11)	0.11 (0.05)		0.02 (0.01)	0.68 (0.15)		
29b θ & θ'(understory + grass + prey-high + hum-live)	8.04	0.01	14	1609.42			0.06 (0.05)	0.03 (0.01)		0.34 (0.22)	-0.04 (0.01)
49 - θ & θ'(d-ag + understory + grass + hum-live)	8.12	0.01	14	1609.51	-0.14 (0.10)		0.06 (0.05)	0.03 (0.01)			-0.04 (0.01)
40 - θ & θ'(H2O + understory + grass + prey-ER)	8.28	0.01	14	1609.66		0.12 (0.05)	0.02 (0.01)	0.02 (0.01)	0.70 (0.15)		
50 - θ & θ'(d-ag + understory + grass + prey-ER + hum-live)	8.81	0.00	15	1606.62							
57b θ & θ'(d-ag + H2O + understory + grass + prey-high + hum-live)	9.11	0.00	16	1603.17							

18 - θ & θ'(d-ag + grass + prey-ER)	9.64	0.00	13	1614.44
50b θ & θ'(d-ag + understory + grass + prey-high + hum-live)	9.84	0.00	15	1607.65
20 - θ & θ'(understory + grass + prey-ER)	10.37	0.00	13	1615.17
54 - θ & θ'(d-ag + H2O + understory + grass + prey-ER)	11.17	0.00	15	1608.98
13 - θ & θ'(H2O + prey-ER)	11.86	0.00	12	1619.94
59 - θ & θ'(prey-ER)	12.56	0.00	11	1623.77
47 - θ & θ'(d-ag + understory + grass + prey-ER)	12.59	0.00	14	1613.98
22 - θ & θ'(H2O + prey-ER + hum-live)	12.68	0.00	13	1617.48
42 - θ & θ'(H2O + understory + prey-ER + hum-live)	13.51	0.00	14	1614.90
38 - θ & θ'(H2O + understory + prey-ER)	13.60	0.00	13	1618.40
62 - θ & θ'(prey-ER + hum-live)	13.68	0.00	12	1621.75
14 - θ & θ'(understory + prey-ER)	13.68	0.00	12	1621.76
23 - θ & θ'(understory + prey-ER + hum-live)	13.91	0.00	13	1618.71
62b θ & θ'(prey-high + hum-live)	14.40	0.00	11	1625.61
31 - θ & θ'(d-ag + H2O + prey-ER)	14.77	0.00	13	1619.57
12 - θ & θ'(d-ag + prey-ER)	14.93	0.00	12	1623.01
34 - θ & θ'(d-ag + H2O + prey-ER +	15.7	0.0	14	1617.

hum-live)	5	0		14
21 - θ & θ'(d-ag + prey-ER + hum-live)	16.19	0.00	13	1620.99
45 - θ & θ'(d-ag + understory + prey-ER)	16.28	0.00	13	1621.08
48 - θ & θ'(d-ag + understory + prey-ER + hum-live)	16.66	0.00	14	1618.04
52 - θ & θ'(d-ag + H2O + understory + prey-ER)	16.68	0.00	14	1618.06
55 - θ & θ'(d-ag + H2O + understory + prey-ER + hum-live)	16.79	0.00	15	1614.59
23b θ & θ'(understory + prey-high + hum-live)	16.81	0.00	13	1621.61
55b θ & θ'(d-ag + H2O + understory + prey-high + hum-live)	17.69	0.00	14	1619.07
47b θ & θ'(d-ag + understory + grass + prey-high)	17.97	0.00	13	1622.78
61b θ & θ'(grass + prey-high)	17.98	0.00	12	1626.06
17 - θ & θ'(understory + hum-live)	18.28	0.00	12	1626.35
42b θ & θ'(H2O + understory + prey-high + hum-live)	18.57	0.00	14	1619.95
18b θ & θ'(d-ag + grass + prey-high)	18.63	0.00	13	1623.43
22b θ & θ'(H2O + prey-high + hum-live)	19.09	0.00	13	1623.89
48b θ & θ'(d-ag + understory + prey-high + hum-live)	19.09	0.00	14	1620.48
21b θ & θ'(d-ag + prey-high + hum-live)	19.41	0.00	13	1624.21
39 - θ & θ'(H2O + understory + hum-live)	19.53	0.00	13	1624.33

19b θ & θ'(H2O + grass + prey-high + hum-live)	19.85	0.00	13	1624.65
46 - θ & θ'(d-ag + understory + hum-live)	19.96	0.00	13	1624.76
20b θ & θ'(understory + grass + prey-high)	20.37	0.00	13	1625.17
33b θ & θ'(d-ag + H2O + grass + prey-high)	20.90	0.00	14	1622.28
60 - θ & θ' (hum-live)	21.31	0.00	11	1632.52
34b θ(d-ag + H2O + prey-high + hum-live)	21.41	0.00	14	1622.79
53 - θ & θ'(d-ag + H2O + understory + hum-live)	21.71	0.00	14	1623.09
59b θ & θ'(prey-high)	22.15	0.00	11	1633.37
16 - θ & θ'(H2O + hum-live)	22.27	0.00	12	1630.35
15 - θ & θ'(d-ag + hum-live)	22.33	0.00	12	1630.40
40b θ & θ'(H2O + understory + grass + prey-high)	22.60	0.00	14	1623.98
9 - θ & θ'(d-ag + grass)	22.89	0.00	12	1630.97
14b θ & θ'(understory + prey-high)	22.93	0.00	12	1631.01
12b θ & θ'(d-ag + prey-high)	23.44	0.00	12	1631.52
58 - θ & θ'(grass)	23.83	0.00	11	1635.04
32 - θ & θ'(d-ag + H2O + hum-live)	23.87	0.00	13	1628.67
54b θ & θ'(d-ag + H2O + understory +	23.9	0.0	15	1621.

grass + prey-high)	8	0		79
13b θ & θ'(H2O + prey-high)	24.75	0.00	12	1632.83
30 - θ & θ'(d-ag + H2O + grass)	24.88	0.00	13	1629.68
44 - θ & θ'(d-ag + understory + grass)	24.96	0.00	13	1629.76
11 - θ & θ'(understory + grass)	25.28	0.00	12	1633.36
10 - θ & θ'(H2O + grass)	25.29	0.00	12	1633.37
38b θ & θ'(H2O + understory + prey-high)	25.81	0.00	13	1630.61
31b θ & θ'(d-ag + H2O + prey-high)	26.34	0.00	13	1631.15
37 - θ & θ'(H2O + understory + grass)	27.22	0.00	13	1632.03
51 - θ & θ'(d-ag + H2O + understory + grass)	27.32	0.00	14	1628.71
52b θ & θ'(d-ag + H2O + understory + prey-high)	27.73	0.00	14	1629.11
4 - θ & θ'(understory)	29.55	0.00	11	1640.77
6 - θ & θ'(d-ag + understory)	30.06	0.00	12	1638.13
θ & θ'(d-ag)	30.51	0.00	11	1641.73
1 - θ & θ'(.)	30.64	0.00	10	1644.86
45b θ & θ'(d-ag + understory + prey-high)	31.58	0.00	15	1629.39
8 - θ & θ'(H2O + understory)	32.27	0.00	12	1640.35

3- θ & θ'(H2O)	33.04	0.00	11	1644.25
5- θ & θ'(d-ag + H2O + understory)	33.08	0.00	13	1637.88
7 - θ & θ'(d-ag + H2O)	33.27	0.00	12	1641.35

Footnotes

a: ψ and *p* structure for all models include: ψ(prey-high + grass + hum-live + grass * hum-live) and *p* (soil + tread).

b: Covariates: d-ag: prevalence of dwellings and agriculture along trail segments; H_2O: prevalence of water bodies along trail segments; understory: prevalence of grassy understory along trail segments; grass: Grassland area in cell; prey-ER: Sum of encounter rates for multiple prey signs (7 species) along 1 km segments within a cell; prey-high: Sum of 'high' intensity encounter rates for multiple prey signs (7 species) along 1 km trail segments within a cell; hum-live: Sum of human and cattle encounter rates along 1 km trail segments within a cell.

For detailed information for covariates, see Table 1.

c: ΔAIC_c is the difference in AIC_c between the best supported model and any given model.

d: *w* is the AIC_c model weight.

e: *K* is the number of parameters

f: -2*l* is twice the negative log likelihood.

Appendix 1.5. Model building strategy to assess covariate influence on tiger occupancy in the CTL.

In the final analysis step, we sought to ascertain how disturbance (human and livestock use, habitat edge) and connectivity covariates would influence tiger occupancy, in additive or multiplicative combinations with *habitat* and *prey* covariates that we had selected in previous steps. A list of models considered follows (Table A-7). A complete table of model selection results and coefficient estimates follows (Table A-8). We note that supported models in Table A-8 are also available in Table 3 of the manuscript.

Table A.7. Covariates included in candidate models representing *a priori* hypotheses about tiger occupancy.

Model #	gras s	prey-high	con n	hum-live	Interaction (hum-live*grass)	hum-live^2	edge-len	NepalDist
1	x							
2		x						
3	x	x						
4			x					
5	x	x	x					
6	x		x					
7		x	x					
8				x				
9						x		
10	x	x		x	x			
11	x			x	x			
12	x	x		x				
13	x			x				
14		x		x				
15							x	
16								x
17	x	x					x	
18	x	x						x
19	x						x	
20	x							x
21		x					x	
22		x						x
23	(.)	(.)	(.)	(.)	(.)		(.)	(.)

Footnotes

a: Covariates: prey-high: High Prey Encounter Rate; ConnStat: habitat connectivity index; grass: grassland area; hum-live: human and livestock encounter rate; NepalDist: distance to international border; edge-len: habitat edge length. The model specification for the parameters θ, θ' and *p* was: θ&θ' (grass + prey-ER + hum-live + H2O), *p* (soil + tread).

Table A1.8. Model selection results and coefficient estimates for all tiger occupancy models

Ψ(grass + NepalDist)	14.2	0.	1	1619				-0.50			0.04	
								Estimated β (SE)				
Model[a]	ΔAICc[b]	w^c	K[d]	$-2l^e$	conn-PA	conn-MUF	prey-high	Grass	hum-live	grass*hum-live	Nepal Dist	edge-len
Ψ(prey-high + conn)	0.00	0.71	2	1601.98	19.84 (1784.43)	1.63 (1.76)	10.15 (4.37)					
Ψ(prey-high + grass + conn)	2.13	0.25	3	1600.84	23.6 (2544.04)	5.35 (5.03)	10.87 (5.12)	0.41 (0.45)				
Ψ(prey-high + grass)	7.49	0.02	1	1612.61			8.77 (4.15)	0.59 (0.43)				
Ψ(prey-high + grass + hum-live)	9.03	0.01	2	1611.01			8.90 (4.83)	0.76 (0.37)	-0.13 (0.10)			
Ψ(prey-high + grass +* hum-live)[f]	10.42	0.00	3	1609.13			7.76 (3.92)	0.07 (0.14)	-0.32 (0.19)	0.12 (0.09)		
Ψ(prey-high + grass + edge-len)	10.62	0.00	2	1612.61			8.82 (4.20)	0.59 (4.20)				0.001 (0.01)
Ψ(prey-high + grass + NepalDist)	10.63	0.00	2	1612.61			8.75 (4.90)	0.59 (0.44)			0.00 (0.03)	
Ψ(conn)	11.24	0.00	1	1616.36	17.42 (2853.03)	-2.10 (1.24)						
Ψ(prey-high)	12.59	0.00	1	1620.73			7.68 (3.26)					
Ψ(grass + conn)	12.72	0.00	2	1614.71	16.34 (1633.92)	-0.67 (1.63)		0.28 (0.28)				
Ψ(grass + hum-live)	13.91	0.00	1	1619.03				0.80 (0.69)	-0.18 (0.11)			
Ψ(grass)	13.94	0.00	1	1622.07				0.54 (0.35)				

	8	00	1	.40		(0.40)			(0.03)		
Ψ(prey-high + hum-live)	14.56	0.00	1	1619.68	7.99 (3.33)		0.05 (0.05)				
Ψ(grass +* hum-live)	14.86	0.00	1	1616.84		0.04 (0.15)	-0.40 (0.20)	0.10 (0.07)			
Ψ(prey-high + NepalDist)	15.56	0.00	1	1620.68	7.34 (2.49)				0.01 (0.03)		
Ψ(prey-high + edge-len)	15.57	0.00	1	1620.69	7.76 (3.32)					-0.00 (0.01)	
Ψ(grass + edge-len)	16.48	0.00	1	1621.60		0.52 (0.58)				0.03 (0.09)	
Ψ(.)	23.89	0.00	9	1634.91							
Ψ(NepalDist)	23.90	0.00	1	1632.03					0.05 (0.04)		
Ψ(hum-live^2)	26.16	0.00	1	1631.28			-0.29 (0.19)				
Ψ(edge-len)	26.39	0.00	1	1634.52						0.03 (0.04)	
Ψ(hum-live)	26.74	0.00	1	1634.87			0.01 (0.04)				

Footnotes

a: Covariates: prey-high: High Prey Encounter Rate; conn: categorical habitat connectivity covariate (three categories No-conn. refers to disconnected patches, conn-PA indexes patches in the CTL connected with Nepal PAs, and conn-MUF indexes patches in the CTL connected with MUFS in Nepal); grass: grassland area; hum-live: human and livestock encounter rate; NepalDist: distance to international border; edge-len: habitat edge length. The model specification for the parameters θ, θ' and p was: $\theta\&\theta'$ (grass + prey-ER + hum-live + H2O), p (soil + tread). The sign "+*" indicates interaction between covariates.

b: ΔAIC_c is the difference in AIC_c between the best supported model and any given model.

c: w is the AIC_c model weight.

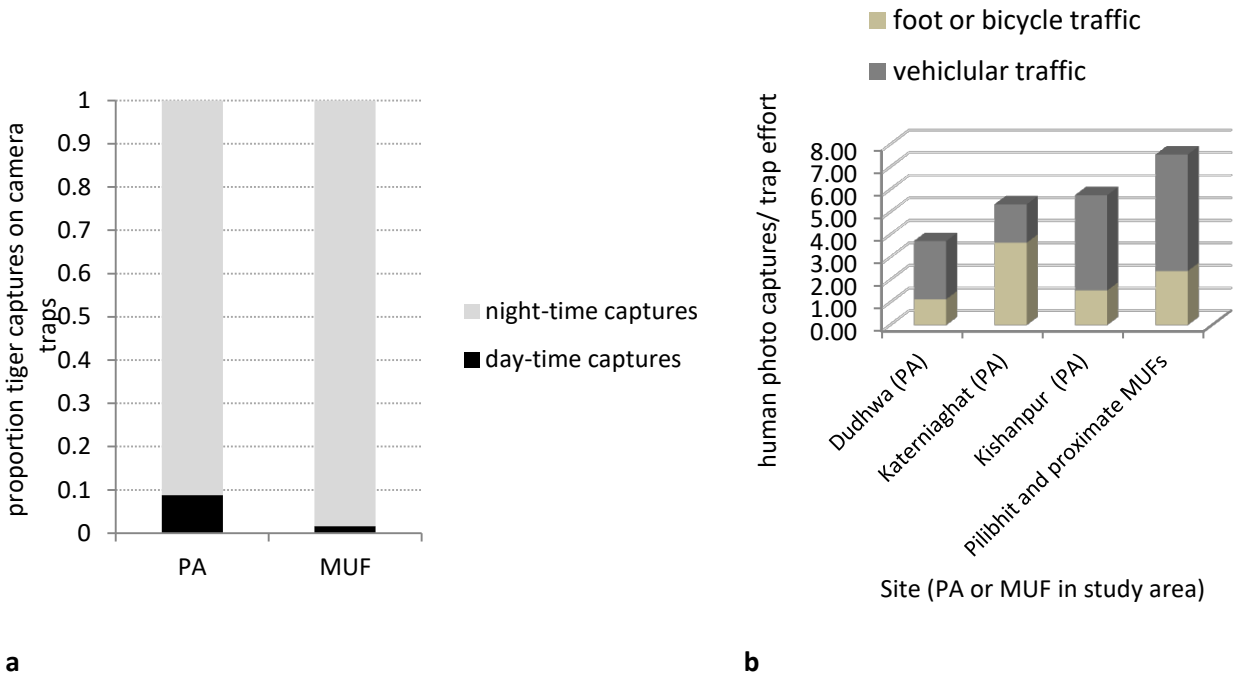
d: K is the number of parameters

e: $-2l$ is twice the negative log likelihood

f: This model represents the best supported global model structure.

Appendix 1.6. Temporal segregation of humans and tigers in protected areas and multiple use forests.

We extensively sampled tiger habitats using camera traps concurrently while carrying out our occupancy surveys (see Chanchani et al., 2014-a for details). While most captures of tigers both in PAs and in MUFs were in the dusk, dawn or night hours, consistent with the species biology, we recorded a higher proportion of daytime (between 8:00 am and 4:30 pm) tiger captures in PAs than in MUFs (Fig. A1-a). These hours represent the period of the day with highest human presence in tiger habitats. We have tallied camera trap images of human use in several PAs and MUFS in the study areas, and note that human use is between 25% and 50% higher in MUFs like Pilibhit Forest Division, than it is in the region's PAs. We suspect that fewer day-time captures in the region's MUFs is likely a consequence of greater day-time human use of such areas. We note that the areas in which we carried out occupancy sampling along trails was larger than the area sampled with camera traps.



a **b**

Fig A1.1-a: Proportion of day-time (8:00 am – 4:30 pm) and night-time captures of tigers on camera traps in three PAs and two MUFs in the Central Terai Landscape. Sample sizes (numbers of photographs) are 1043 and 245 for PAs and MUFs respectively. PAs in this figure include Dudhwa National Park, and Kishanpur and Katerniaghat Wildlife Sanctuaries, and MUFs include Pilibhit and Surai (Terai East) Forest Divisions. Figure A1-b provides an index of the relative abundance of humans on forest roads and trails in PAs and MUFs in the CTL, based on camera trap data. While we followed a consistent sampling design (trap spacing, paired camera traps) at all locations, trap effort varied between sites (see Chanchani et al., 2014-a). We adjusted the count of photographs in each category by the total sampling effort, measured as the number of trap nights in a given site, eg. Pilibhit Forest Division. This figure is based on > 80,000 photo-captures of humans from >600 camera traps stations distributed over tiger habitats in the CTL in 2013.

Appendix 2.1. Preparation of prey density covariate.

We considered five covariates in for our secr models to estimate tiger density: prey density, percent canopy cover, distance to large grasslands, distance to habitat edges, and distance to the international (Nepal-India) border. All covariates were spatially explicit, i.e. covariates were available for all locations within the habitat integration region in our SECR models.

The prey covariate was derived by using density surface modeling (Miller et al., 2013). We adopted a two step procedure. In the first step, the 'combined' abundance of 6 ungulate species (chital, nilgai, hog deer, wild pigs, barking deer and sambar) was estimated using distance sampling (Buckland et al., 2001). This enabled us to account for the imperfect detection process (not all animals present along transect lines are detected). Data was combined for all 6 species because we had few (<20) detections of some 'habitat specialist' species such as swamp deer occur which in high densities in small areas (riparian grasslands) within the study area. For details of line transect sampling and species and site-specific summaries of detections along transect lines, refer to chapter 4 Chanchani et al., 2014 (available online). We modeled the influence of a single covariate ("grazed") on detection probability in our distance analysis and fit several variations of detection functions (half normal, cosine, and hazard rate) with polynomial term adjustments. The covariate grazed distinguished tall grasslands from short grasslands (which were frequently grazed by livestock from forest-edge villages). We discriminated between candidate models using AICc (Burnham and Anderson., 2004) and selected the best supported model was a half normal model with 2 polynomial cosine terms. The inclusion of the covariate "grazed" was not supported.

Analyses were carried out in the Distance package in R (Miller, 2012). Abundance was estimated separately for each of many 200m contiguous "segments" along transect lines. Segment lengths were short enough such that we did not expect a large change in covariate values or density within a segment. We used a right truncation distance of160 m in our Distance analyses.

In the second analysis step generalized additive models (GAMs) were fitted to the abundances derived from the distance analysis in step 1. We considered 7 environmental/ management covariates for this analysis: namely, distance to grasslands, distance to forest edge, % tree canopy cover, "poaching threat", *Teliocora acuminata* (unpalatable weedy species) abundance, Normalized Difference Vegetation Index (a measure of plant productivity), distance to water and protection status (PA or MUF). Covariates for the GAM models were all spatially referenced, and only uncorrelated variables ($R<0.5$) were included in models. Covariate information was ascribed to each 200 m segment along transect lines. To predict prey density beyond sampled locations, covariates were assigned to a grid evenly spaced points (580 m apart). Estimated abundance of ungulates was modeled for detections of all ungulates (combined) for each transect segment as a sum of smooth functions of the covariates using a GAM (Winiarski et al, 2014). To fit models and determine variable importance, we adopted a 'forward-backward' covariate selection procedure (Pearce and Ferrier, 2000, Harihar et al, 2014). Each forward step was succeeded by a backward step in which we eliminated variables in the models that were no longer significant. We used GCV scores and percent deviance explained to compare between models. Models that used a Tweedie distribution to model the segment abundance data were supported, relative to models where the abundance (count) data followed a Poisson distribution. The model that we finally selected to model prey density (a covariate for our tiger SECR models) had the structure: N(DistIntBorder + DistGrass + DistEdge + PercentTreeCov + NDVI. The

listed covariates are distance to international border, distance to grasslands, distance to habitat edges, percent tree cover and NDVI respectively.

Data sources and processing of the 4 other covariates are described in Table2 in the manuscript.

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Appendix 2.2. Result summary from global models to ascertain the best supported combination of detection (σ, $g0/a_0$) parameters.

Table A2.1 Summary of model selection results for global models (Δ AICc and model weight) for 8 model sets representing sites sampled in 2012 and 2013. In all models, a 'global' model structure (D(Grass + Prey + EdgeDist + TreeCov) was used to model variation in density. ΔAICc and AICc weights (in parentheses) are reported for 6 alternate parameterizations of detection parameters (columns). Models that garnered high AICc support are in bold.

Site/ model	g_0(sex) σ(sex) pmix(sex)	g_0(.) σ(sex) pmix(sex)	g_0(sex) σ(.) pmix(sex)	g_0(.) σ(.) pmix(sex)	a_0(.) σ(.) pmix(sex)	a_0(.) σ(sex) pmix(sex)
No. of parameters	10	9	9	8	8	9
Dudhwa NP '12	31.53(0)	**0(1)**	36.03(0)	21.61(0)	27.03(0)	16(0)
Dudhwa NP '13	21.61(0)	**0(0.98)**	31.53(0)	16(0)	16(0)	8.08(0.02)
Katerniaghat WLS '12	8.45(0.01)	2.25(0.24)	8.33(0.01)	**0(0.74)**	181.82(0)	190.15(0)
Katerniaghat WLS '13	5.94(0.05)	**0(0.95)**	78.88(0)	69.39(0)	381.24(0)	372.2(0)
Kishanpur WLS '12	8.51(0.01)	**0(0.99)**	69.92(0)	79.22(0)	79.22(0)	58.65(0)
Kishanpur WLS '13	14.42(0)	13.09(0)	21.84(0)	12.54(0)	12.54(0)	**0(1)**
Pilibhit RF '13	3.69(0.08)	9.91(0)	5.53(0.03)	2.03(0.19)	2.03(0.19)	**0(0.51)**
Pilibhit Forest Complex '13	**0(1)**	26.01(0)	137.75(0)	135.63(0)	136.32(0)	28.88(0)

Table A2.2.Estimates of tiger density (individuals/100 km^2) and associated standard errors and confidence intervals (in parentheses) for global models with alternate parameterizations of detection parameters (σ, g_0/a_0). In all models, a 'global' model structure (D(Grass + Prey + EdgeDist + TreeCov) was used to model variation in density. ΔAICc and AICc weights (in parentheses) are reported for 6 alternate parameterizations of detection parameters (columns). Models that garnered high AICc support for each site are in bold text. [++] DNP: Dudhwa NP, Kghat: Katerniaghat WLS, Kpur: Kishanpur WLS, PRF: Pilibhit Reserve Forest, PFC: Pilibhit Forest Complex.

Site and year[++]	$\widehat{D}$ g_0(sex), σ(sex)]	$\widehat{D}$ g_0(.), σ(sex)	$\widehat{D}$ g_0(sex), σ(.)	$\widehat{D}$ g_0(.), σ(.)	$\widehat{D}$ a_0(.), σ(.)	$\widehat{D}$ a_0(.), σ(sex)
DNP '13	3.13;1.08 (1.62-6.05)	**3.15;1.08 (1.64-6.04)**	2.14;1.31 (0.71-6.47)	2.2;1.11 (0.86-5.6)	1.97;1.59 (0.49-7.91)	2.99;1.06 (1.53-5.86)
DNP '12	0.72;0.84 (0.12-4.45)	**0.57;1.11 (0.05-6.65)**	0.38;1.08 (0.02-7)	0.5;1.11 (0.04-6.87)	0.5;1.11 (0.04-6.87)	0.52;0.73 (0.07-3.98)
Kghat '13	3.13;1.08 (1.62-6.05)	3.15;1.08 (1.64-6.04)	2.14;1.31 (0.71-6.47)	**2.2;1.11 (0.86-5.6)**	1.97;1.59 (0.49-7.91)	2.99;1.06 (1.53-5.86)
Kghat '12	3.78;2.52 (1.15-12.39)	**3.95;2.66 (1.19-13.11)**	4.2;2.2 (1.6-11.02)	4.2;2.21 (1.6-11.06)	1.22;167.63 (0-571.1)	0.52;0.73 (0.07-3.98)
Kpur '13	5.1;1.65 (2.75-9.45)	**5.31;1.66 (2.92-9.68)**	5.43;1.65 (3.03-9.71)	5.46;1.64 (3.07-9.71)	5.46;1.64 (3.07-9.71)	5.21;1.69 (2.81-9.68)
Kpur '12	4.47;1.67 (2.2-	4.48;1.67 (2.21-	3.76;1.49 (1.78-	3.53;1.39 (1.68-	3.53;1.39 (1.68-	**3.83;1.49 (1.84-**

	9.09)	9.08)	7.94)	7.43)	7.43)	**7.99)**
PRF ‘3	2.99;1.15 (1.44-6.19)	2.35;1.29 (0.86-6.41)	2.67;0.82 (1.48-4.81)	2.73;0.78 (1.58-4.71)	2.55;0.85 (1.35-4.83)	**2.51;0.94 (1.23-5.11)**
PFC ’13	**3.27;0.62 (2.26-4.73)**	3.17;0.64 (2.15-4.7)	2.64;0.77 (1.51-4.61)	2.55;0.69 (1.51-4.29)	2.51;0.72 (1.45-4.36)	3.01;0.67 (1.95-4.64)

Table A2.3. Estimates of the baseline encounter probability detection parameter ($g_{0/}$ a_0) and associated standard errors and confidence intervals (in parentheses) for global models with alternate parameterizations of detection parameters (σ, g_0/a_0). In all models, a 'global' model structure (D(Grass + Prey + EdgeDist + TreeCov) was used to model variation in density. ΔAICc and AICc weights (in parentheses) are reported for 6 alternate parameterizations of detection parameters (columns). Models that garnered high AICc support for each site are in bold text.

Site and year Sex		Estimates of the baseline encounter probability (g_0) associated with models with the following detection parameterizations					
		g_0 (sex), σ(sex)	g_0 (.), σ(sex)	g_0 (sex), σ(.)	g_0 (.), σ(.)	a_0 (.), σ(sex)	a_0 (.), σ(sex)
DNP '13	F	0.07;0.02(0.05-0.11)	**0.04;0.01(0.03-0.05)**	0.03;0.01(0.02-0.04)	0.03;0(0.03-0.04)	371.53;46.93(290.34-475.42)	288.38;33.5(229.83-361.85)
DNP '13	M	0.03;0.01(0.02-0.04)	**0.04;0.01(0.03-0.05)**	0.04;0.01(0.03-0.05)	0.03;0(0.03-0.04)	371.53;46.93(290.34-475.42)	288.38;33.5(229.83-361.85)
DNP '12	F	0.07;0.02(0.05-0.11)	**0.04;0.01(0.03-0.05)**	0.03;0.01(0.02-0.04)	0.03;0(0.03-0.04)	390.48;46.92(308.81-493.77)	318.86;41.32(247.6-410.62)
DNP '12	M	0.03;0.01(0.02-0.04)	**0.04;0.01(0.03-0.05)**	0.04;0.01(0.03-0.05)	0.03;0(0.03-0.04)	390.48;46.92(308.81-493.77)	318.86;41.32(247.6-410.62)
Kghat '13	F	0.06;0.01(0.05-0.08)	0.05;0.01(0.04-0.06)	0.04;0.01(0.03-0.06)	**0.04;0.01(0.03-0.06)**	1010.04;138.91(772.36-1320.84)	14598.43;1609.63(11768.89-18108.25)
Kghat '13	M	0.04;0.01(0.03-0.05)	0.05;0.01(0.04-0.06)	0.05;0.01(0.03-0.06)	**0.04;0.01(0.03-0.06)**	1010.04;138.91(772.36-1320.84)	14598.43;1609.63(11768.89-18108.25)
Kghat '12	F	0.06;0.02(0.04-0.1)	**0.04;0.01(0.03-0.06)**	0.04;0.01(0.03-0.06)	0.04;0.01(0.03-0.05)	3849.08;884.64(2467.38-6004.52)	4810.11;1052.72(3148.04-7349.72)
Kghat '12	M	0.03;0.01(0.02-0.05)	**0.04;0.01(0.03-0.06)**	0.04;0.01(0.02-0.05)	0.04;0.01(0.03-0.05)	3849.08;884.64(2467.38-6004.52)	4810.11;1052.72(3148.04-7349.72)
Kpur '13	F	0.11;0.01(0.08-0.13)	**0.08;0.01(0.07-0.09)**	0.09;0.01(0.07-0.11)	0.08;0.01(0.07-0.09)	221.27;18.63(187.67-260.9)	207.03;23.03(166.58-257.3)

Kpur '13	M	0.05;0.01(0.04-0.07)	**0.08;0.01(0.07-0.09)**	0.07;0.01(0.05-0.09)	0.08;0.01(0.07-0.09)	221.27;18.63(187.67-260.9)	207.03;23.03(166.58-257.3)
Kpur '12	F	0.06;0.01(0.05-0.08)	0.06;0.01(0.05-0.07)	0.03;0(0.03-0.04)	0.05;0(0.04-0.06)	302.11;26.29(254.82-358.19)	**237.61;18.46(204.09-276.63)**
Kpur '12	M	0.05;0.01(0.04-0.07)	0.06;0.01(0.05-0.07)	0.07;0.01(0.05-0.08)	0.05;0(0.04-0.06)	302.11;26.29(254.82-358.19)	**237.61;18.46(204.09-276.63)**
Pili '13	F	0.03;0.01(0.02-0.05)	0.03;0(0.02-0.04)	0.02;0(0.01-0.03)	0.02;0(0.02-0.03)	157.97;26.17(114.42-218.09)	**135.31;19.96(101.49-180.39)**
Pili '13	M	0.02;0.01(0.02-0.04)	0.03;0(0.02-0.04)	0.03;0.01(0.02-0.04)	0.02;0(0.02-0.03)	157.97;26.17(114.42-218.09)	**135.31;19.96(101.49-180.39)**
PFC '13	F	**0.07;0.01(0.05-0.08)**	0.05;0(0.04-0.05)	0.03;0(0.03-0.04)	0.04;0(0.03-0.05)	226.86;14.26(200.59-256.57)	210.17;14.17(184.18-239.83)
PFC '13	M	**0.03;0(0.02-0.04)**	0.05;0(0.04-0.05)	0.04;0(0.04-0.05)	0.04;0(0.03-0.05)	226.86;14.26(200.59-256.57)	210.17;14.17(184.18-239.83)

[++] DNP: Dudhwa NP, Kghat: Katerniaghat WLS, Kpur: Kishanpur WLS, PRF: Pilibhit Reserve Forest, PFC: Pilibhit Forest Complex.

Table A2.4. Estimates of the scale detection parameter (σ) and associated standard errors and confidence intervals (in parentheses) for global models with alternate parameterizations of detection parameters (σ, $g0/a_0$). In all models, a 'global' model structure (D(Grass + Prey + EdgeDist + TreeCov) was used to model variation in density. ΔAICc and AICc weights (in parentheses) are reported for 6 alternate parameterizations of detection parameters (columns). Models that garnered high AICc support for each site are in bold text. .

Site and year	Sex	Estimates of the scale parameter (σ) associated with models with the following detection parameterizations					
		g0(sex), σ(sex)	g0(.), σ(sex)	g0(sex), σ(.)	g0(.), σ(.)	ao(.), σ(.)	ao(.), σ(sex)
DNP '13	F	2016.73;187.48 (1681.47-2418.85)	**2369.35;215.57 (1983.1-2830.83)**	4174.47;239.31 (3731.17-4670.43)	4253.21;250.18 (3790.46-4772.47)	4175.78;242.5 (3726.89-4678.73)	2157.37;234.15(1745.06-2667.1)
DNP '13	M	4964.95;401.28 (4238.68-5815.67)	**4580.7;306.36 (4018.51-5221.53)**	4174.47;239.31 (3731.17-4670.43)	4253.21;250.18 (3790.46-4772.47)	4175.78;242.5 (3726.89-4678.73)	4640.23;324.96(4045.78-5322.03)
DNP '12	F	2016.73;187.48 (1681.47-2418.85)	**2369.35;215.57 (1983.1-2830.83)**	4174.47;239.31 (3731.17-4670.43)	4175.77;242.35 (3727.16-4678.39)	4253.22;250.27 (3790.29-4772.68)	2419.21;300.11(1898.82-3082.22)
DNP '12	M	4964.95;401.28 (4238.68-5815.67)	**4580.7;306.37 (4018.51-5221.53)**	4174.47;239.31 (3731.17-4670.43)	4175.77;242.35 (3727.16-4678.39)	4253.22;250.27 (3790.29-4772.68)	4714.15;326.77(4115.96-5399.27)
Kghat '13	F	2800.22;192.25 (2448.05-3203.05)	2993.33;195 (2634.88-3400.54)	6062;319.18(5468.01-6720.53)	**6063.15;306.62 (5491.36-6694.47)**	6035.53;298.37 (5478.5-6649.19)	47008.75;3753.77 (40208.33-54959.31)
Kghat '13	M	7337.33;447.6(6511.19-8268.3)	6968.79;367.71 (6284.56-7727.52)	6062;319.18(5468.01-6720.53)	**6063.15;306.62 (5491.36-6694.47)**	6035.53;298.37 (5478.5-6649.19)	22018.25;1843.52 (18691.26-25937.42)
Kghat '12	F	1620.85;190.74 (1288-2039.71)	**1842.15;204.74 (1482.57-2288.96)**	2245.25;181.27 (1917.15-2629.5)	2246.43;184.53 (1912.9-2638.13)	17370.64;1787.04 (14206.17-21240.01)	16627.02;1754.11 (13528.92-20434.57)
Kgha	M	2867.06;323.96	**2714.66;272.96**	2245.25;181.27	2246.43;184.53	17370.64;1787.04	25091.74;4265.95

t ‘12		(2299.12-3575.29)	**(2230.18-3304.38)**	(1917.15-2629.5)	(1912.9-2638.13)	(14206.17-21240.01)	(18023.71-34931.51)
Kpur ‘13	F	1650.85;94.66 (1475.5-1847.04)	**1809.14;113.31 (1600.33-2045.19)**	2091.97;84.29 (1933.19-2263.79)	2096.16;87.41 (1931.71-2274.6)	2089.45;86.14 (1927.34-2265.21)	1694.02;134.32(1450.55-1978.37)
Kpur ‘13	M	2648.4;198.21 (2287.53-3066.21)	**2364.98;144.75 (2097.88-2666.1)**	2091.97;84.29 (1933.19-2263.79)	2096.16;87.41(1931.71-2274.6)	2089.45;86.14 (1927.34-2265.21)	2538.26;173.2 (2220.86-2901.01)
Kpur ‘12	F	1810.9;107.79 (1611.66-2034.78)	1857.61;102.47 (1667.37-2069.54)	2997.51;141.08 (2733.51-3287)	3107.73;133.6 (2856.71-3380.8)	3107.61;133.96 (2855.95-3381.44)	**1981.15;126.27 (1748.73-2244.47)**
Kpur ‘12	M	4140.04;296.96 (3597.72-4764.1)	4044.09;258.61 (3568.16-4583.51)	2997.51;141.08 (2733.51-3287)	3107.73;133.6 (2856.71-3380.8)	3107.61;133.96 (2855.95-3381.44)	**3398.36;170.7 (3079.93-3749.7)**
Pili ’13	F	2194.54;257.69(1744.76-2760.27)	2010.14;182.26 (1683.46-2400.2)	3303.35;278.61 (2800.84-3896.01)	3311.58;281.55 (2804.12-3910.86)	3320.12;284.58 (2807.54-3926.27)	**2339.47;292.59 (1832.62-2986.5)**
Pili ‘13	M	4061.47;453.21 (3265.82-5050.96)	4176.97;416.92 (3436.44-5077.07)	3303.35;278.61 (2800.84-3896.01)	3311.58;281.55 (2804.12-3910.86)	3320.12;284.58 (2807.54-3926.27)	**3639.43;346.06 (3021.88-4383.18)**
PFC ‘13	F	**1873.06;88.95 (1706.68-2055.67)**	2091.07;93.89 (1914.99-2283.34)	3012.21;99.68 (2823.08-3214)	3000.43;98.42 (2813.65-3199.6)	3000.1;98.44 (2813.28-3199.32)	2000.08;87.68 (1835.48-2179.45)
PFC ’13	M	**4171.74;223.06 (3756.96-4632.32)**	3717.41;162.05 (3413.12-4048.82)	3012.21;99.68 (2823.08-3214)	3000.43;98.42 (2813.65-3199.6)	3000.1;98.44 (2813.28-3199.32)	3878.05;184.77 (3532.5-4257.41)

Footnotes:

These are not the "final" σ estimates reported in the Chapter 2. The best supported detection covariate structure for each site from these global models was carried forward into step 2 of or analysis, wherein we tested specific ecological hypotheses (about spatial heterogeneity in tiger density as a function of covariates). σ estimates from those models are the 'final' estimates reported in the paper, and have been reported in Appendix 3. [++] DNP: Dudhwa NP, Kghat: Katerniaghat WLS, Kpur: Kishanpur WLS, PRF: Pilibhit Reserve Forest, PFC: Pilibhit Forest Complex.

Appendix 2.3. Site and year specific estimates of density, abundance and detection parameters from step 2 of the analysis (modeling spatial heterogeneity in tiger density as a function of covariates).

Table A2.5 Eight sets of site and year specific estimates of model selection scores, abundance, density and associated uncertainty. Density for inhomogeneous models was computed at the median values of covariates associated with each site (provided in footnotes). For each of the 8 model set, parameterization of detection parameters was held constant based on the best supported covariate structure ascertained in analysis step 1 (detailed results are in appendix 2). Covariate legend: Grass - distance to large grasslands; TreeCov = % tree canopy cover; Edge = distance to edge of primary habitat area; Prey- prey density for 6 ungulate species.

No.	***Model***	***npar***	***Δ AIC; AICc weight;Log likelihood***	***$\widehat{N}$;estimate; se; lcl-ucl)***	***$\widehat{D}$;estimate; se; lcl-ucl)***	***No.***	***Model***	***Npar***	***Δ AIC; AICc weight;Log likelihood***	***$\widehat{N}$; se; lcl-ucl***	***$\widehat{D}$; se; lcl-ucl***
			DNP 2012						**DNP 2013**		
15	D(1)	5	**0;0.4;-369.67**	14.24;0.5; (14.02-17.02)	2.05;0.56; (1.21-3.48)	4	D~Prey	6	**0;0.85; -635.87**	14.17;0.42; (14-16.64)	0.6;0.29; (0.25-1.47)
2	D(TreeCov)	6	**0.99;0.25; -366.91**	14.42;0.68; (14.05-17.89)	1.83;0.78; (0.82-4.09)	6	D~Prey + TreeCov	7	5.05;0.07; -634.07	14.35;0.63; (14-17.67)	0.75;0.38; (0.29-1.92)
4	D(Prey)	6	**0.99;0.25; -366.91**	14.13;0.36; (14.01-	1.18;0.49; (0.54-	2	D~TreeCov	6	6.79;0.03; -639.27	15.1;1.13; (14.2-	1.21;0.6; (0.48-

				16.34)	2.59)					19.81)	3.05)
1	D(Grass)	6	4.25;0.05; -368.54	14.08;0.3; (14-15.99)	0.3;1.87; (0.01-12.9)	5	D~Prey + Grass	7	6.62;0.03; -634.85	14.19;0.45; (14-16.78)	0.76;0.41; (0.28-2.04)
8	D(Edge)	6	5.8;0.02; -369.32	14.3;0.57; (14.03-17.35)	2.25;0.65; (1.3-3.91)	13	D~Edge 1 + Prey	7	7.56;0.02; -635.32	14.27;0.54; (14-17.26)	0.89;0.39; (0.39-2.04)
3	D(TreeCov + Grass)	7	7.72;0.01; -365.94	14.19;0.46; (14.01-16.9)	0.57;0.94; (0.06-5.42)	1	D~Grass	6	21;0; -646.37	14.52;0.74; (14.1-18.11)	1.48;0.89; (0.5-4.38)
6	D(Prey + TreeCov)	7	8.13;0.01; -366.15	14.25;0.53; (14.02-17.25)	1.56;0.66; (0.71-3.45)	3	D~TreeCov + Grass	7	13.93;0; -638.5	14.94;1.05; (14.2-19.48)	0.64;0.62; (0.13-3.13)
10	D(Edge + TreeCov	7	7.35;0.01; -365.76	14.42;0.69; (14.04-17.93)	0.74;0.96; (0.1-5.21)	7	D~Prey+ TreeCov + Grass	8	16.51;0; -633.72	14.33;0.61; (14-17.57)	2.01;0.58; (1.16-3.49)
5	D(Prey + Grass)	7	9.65;0; -366.91	14.12;0.36; (14.01-16.34)	1.36;0.54; (0.64-2.89)	8	D~Edge	6	17.02;0; -644.38	14.94;1.03; (14.2-19.38)	1.9;0.58; (1.06-3.4)
7	D(Prey+ TreeCov + Grass)	8	19.71;0; -365.87	14.18;0.45; (14.01-16.86)	1.35;0.88; (0.42-4.32)	9	D~Grass + Edge	7	24.41;0; -643.74	14.86;0.99; (14.1-19.19)	0.88;0.73; (0.21-3.62)
9	D(Grass +	7	11.88;0;	14.12;0.36; (14.01-	1.43;0.94; (0.44-	10	D~Edge +	7	14.82;0;	15.05;1.11; (14.2-	0.7;0.32;

	Edge)		-368.02	16.36)	4.64)		TreeCov		-638.95	19.75)	(0.3-1.67)
11	D(Edge +* Grass)	8	19.55;0; -365.79	14.28;0.56; (14.02-17.4)	0.12;20.32 ; (0-64.46)	11	D~Edge +* Grass	8	36.03;0; -643.49	14.28;0.56; (14-17.4)	1.49;1.38; (0.32-6.97)
12	D(Edge + TreeCov + Grass)	8	18.32;0; -365.17	14.28;0.56; (14.02-17.4)	0.52;1.04; (0.04-6.23)	12	D~Edge + TreeCov + Grass	8	25.82;0; -638.38	14.28;0.56; (14-17.4)	0.79;0.75; (0.16-3.8)
13	D(Edge1 + Prey	7	9.54;0; -366.85	14.15;0.39; (14.01-16.52)	1.47;0.61; (0.67-3.23)	14	D~Global	9	34.42;0 ;-633.58	14.22;0.5; (14-17.14)	0.57;1.11; (0.05-6.65)
14	D(Global)	9	36.44;0; -365.13	14.22;0.5; (14.01-17.14)	0.57;1.11; (0.05-6.65)	15	D~1	5	14.8;0; -646.52	14.56;0.77; (14.1-18.22)	1.88;0.52; (1.11-3.19)
No.	*Model*	*npar*	*Δ AIC; AICc weight;Log likelihood*	*$\widehat{N}$;estimate; se; lcl-ucl)*	*$\widehat{D}$;estimate; se; lcl-ucl)*	*No.*	*Model*	*npar*	*Δ AIC; AICc weight;Log likelihood*	*$\widehat{N}$; se; lcl-ucl*	*$\widehat{D}$; se; lcl-ucl*
			Kghat-2012						**Kghat_2013**		
1	D(Grass)	5	**0;0.48;-228.76**	18.55;0.78; (18.07-22.32)	1.55;1.26; (0.39-6.24)	15	D(1)	5	**0;0.49;-448.29**	17.12;0.34; (17.01-19.24)	2.87;0.72; (1.78-4.65)
3	D(TreeCov + Grass)	6	**2.01;0.17; -227.44**	18.49;0.73; (18.06-22.1)	0.52;0.93; (0.05-	8	D(Edge)	6	**2.38;0.15;-447**	17.13;0.37; (17.01-	3.13;0.8; (1.92-

					5.41)
15	D(1)	4	**2.58;0.13; -232.01**	22.18;2.29; (19.53-29.4)	4.76;1.14; (2.99-7.57)
5	D(Prey + Grass)	6	3.39;0.09; -228.13	18.47;0.72; (18.06-22.06)	5.25;1.38; (3.16-8.73)
9	D(Grass + Edge)	6	4.57;0.05; -228.72	18.55;0.78; (18.07-22.29)	4.6;1.68; (2.3-9.18)
2	D(TreeCov)	5	6.27;0.02; -231.89	22.2;2.3; (19.54-29.45)	4.84;1.16; (3.04-7.7)
4	D(Prey)	5	6.5;0.02; -232.01	22.11;2.41; (19.42-29.91)	4.81;1.34; (2.82-8.22)
8	D(Edge)	5	6.03;0.02; -231.77	21.63;2.25; (19.18-29.12)	3.93;1.62; (1.81-8.53)
7	D(Prey+ TreeCov + Grass)	7	7.45;0.01; -227.38	18.47;0.72; (18.06-22.05)	4.06;1.89; (1.7-9.69)
12	D(Edge + TreeCov +	7	7.56;0.01;	18.54;0.78; (18.07-	3.79;1.79; (1.57-

				19.37)	5.12)
4	D(Prey)	6	**2.96;0.11;-447.29**	17.14;0.38; (17.01-19.43)	2.11;0.77; (1.05-4.2)
2	D(TreeCov)	6	**3.21;0.1;-447.42**	17.11;0.33; (17.01-19.15)	2.78;0.88; (1.52-5.08)
1	D(Grass)	6	3.65;0.08;-447.64	17.05;0.23; (17-18.6)	2.76;0.73; (1.66-4.58)
9	D(Grass + Edge)	7	6.31;0.02;-445.94	17.05;0.23; (17-18.57)	3.71;1.01; (2.2-6.25)
3	D(TreeCov + Grass)	7	8.17;0.01;-446.88	17.05;0.24; (17-18.61)	2.75;0.83; (1.54-4.91)
5	D(Prey + Grass)	7	7.46;0.01;-446.52	17.06;0.26; (17-18.75)	2.62;0.86; (1.4-4.92)
6	D(Prey + TreeCov)	7	8.49;0.01;-447.03	17.13;0.36; (17.01-19.33)	2.49;0.81; (1.34-4.65)
10	D(Edge +	7	7.7;0.01;-	17.12;0.35; (17.01-	2.98;0.95;

	Grass)		-227.44	22.29)	9.14)		TreeCov)		446.64	19.25)	(1.61-5.5)
6	D(Prey + TreeCov)	6	10.69;0; -231.78	21.81;2.31; (19.27-29.42)	4.99;1.24; (3.09-8.06)	13	D(Edge1 + Prey)	7	7.34;0.01;-446.46	17.08;0.29; (17-18.93)	2.63;0.86; (1.41-4.9)
10	D(Edge + TreeCov)	6	10.23;0; -231.55	21.6;2.23; (19.18-28.98)	3.9;1.57; (1.82-8.35)	7	D(Prey+ TreeCov + Grass)	8	14.64;0;-446.33	17.06;0.25; (17-18.72)	2.79;0.94; (1.47-5.31)
11	D(Edge +* Grass)	7	10.04;0; -228.68	18.54;0.78; (18.07-22.29)	4.44;1.79; (2.07-9.51)	11	D(Edge +* Grass)	8	10.83;0;-444.43	17.08;0.29; (17-18.93)	2.83;1.62; (1-8.05)
13	D(Edge1 + Prey)	6	10.66;0; -231.77	21.67;2.33; (19.17-29.47)	3.89;1.71; (1.7-8.88)	12	D(Edge + TreeCov + Grass)	8	13.47;0;-445.75	17.15;0.39; (17.01-19.51)	3.59;1.16; (1.94-6.65)
14	D(Global)	8	14.22;0; -227.37	18.48;0.72; (18.06-22.07)	4.2;2.21; (1.6-11.07)	14	D(Global	9	22.22;0;-445.27	17.06;0.25; (17-18.67)	3.15;1.08; (1.64-6.04)
No.	*Model*	*npar*	*Δ AIC; AICc weight;Log likelihood*	*$\widehat{N}$;estimate; se; lcl-ucl)*	*$\widehat{D}$;estimate; se; lcl-ucl)*	*No.*	*Model*	*npar*	*Δ AIC; AICc weight;Log likelihood*	*$\widehat{N}$; se; lcl-ucl*	*$\widehat{D}$; se; lcl-ucl*
			Kpur_2012						**Kpur 2013**		
15	D(1)	4	**0;0.38;**	19;0.07;	5.45;1.29; (3.45-	15	D(1)	5	**0;0.76;-**	16;0.03;	4.97;1.27; (3.04-

			-502.71	(19-19.44)	8.61)				**431.18**	(16-16.14)	8.12)
2	D(TreeCov)	5	**0.13;0.36; -500.58**	19.01;0.1; (19-19.64)	4.45;1.32; (2.52-7.87)	2	D(TreeCov)	6	4.89;0.07;-430.95	16;0.03; (16-16.13)	8.06;6.96; (1.87-34.79)
1	D(Grass)	5	4.22;0.05; -502.63	19.01;0.07; (19-19.46)	3.43;6.33; (0.32-37.35)	1	D(Grass)	6	5.18;0.06;-431.1	16;0.03; (16-16.14)	5.15;1.36; (3.1-8.56)
4	D(Prey)	5	3.93;0.05; -502.48	19.01;0.08; (19-19.56)	4.85;1.38; (2.81-8.39)	8	D(Edge)	6	4.97;0.06;-431	16;0.02; (16-16.13)	5.65;2.45; (2.5-12.74)
8	D(Edge)	5	4;0.05; -502.52	19;0.07; (19-19.45)	5.83;1.48; (3.57-9.51)	4	D(Prey)	6	5.47;0.05;-431.24	16;0.03; (16-16.14)	5;2.05; (2.31-10.83)
6	D(Prey + TreeCov)	6	4.79;0.04; -500.32	19.01;0.07; (19-19.48)	4.35;1.36; (2.4-7.91)	3	D(TreeCov + Grass)	7	11.47;0;-430.91	16;0.03; (16-16.13)	7.99;7.01; (1.82-35.14)
3	D(TreeCov + Grass)	6	5.29;0.03; -500.57	19.01;0.1; (19-19.65)	3.73;6.02; (0.41-34.31)	5	D(Prey + Grass)	7	11.84;0;-431.1	16;0.03; (16-16.14)	5.08;2.17; (2.28-11.31)
10	D(Edge + TreeCov)	6	5.28;0.03; -500.57	19.01;0.1; (19-19.65)	4.32;1.54; (2.19-8.49)	6	D(Prey + TreeCov)	7	11.44;0;-430.9	16;0.02; (16-16.13)	8.45;7.46; (1.91-37.44)
5	D(Prey +	6	8.99;0;	19.01;0.09;	5.23;1.29; (3.25-	7	D(Prey+ TreeCov	8	19.89;0;-	16;0.02;	8.46;7.62; (1.87-

	Grass)		-502.42	(19-19.57)	8.42)		+ Grass)		430.84	(16-16.13)	38.3)
7	D(Prey+ TreeCov + Grass)	7	10.94;0; -500.29	19.01;0.07; (19-19.48)	4.33;1.36; (2.38-7.88)	9	D(Grass + Edge)	7	11.44;0;-430.9	16;0.02; (16-16.12)	6.11;2.75; (2.63-14.19)
9	D(Grass + Edge)	6	8.82;0; -502.33	19.01;0.07; (19-19.48)	5.83;1.48; (3.58-9.5)	10	D(Edge + TreeCov)	7	11.43;0;-430.89	16;0.02; (16-16.12)	8.14;7.05; (1.88-35.26)
11	D(Edge +* Grass)	7	14.62;0; -502.12	19.01;0.07; (19-19.47)	5.56;1.53; (3.28-9.45)	11	D(Edge +* Grass)	8	19.93;0;-430.85	16;0.02; (16-16.11)	6.69;3.57; (2.51-17.86)
12	D(Edge + TreeCov + Grass)	7	11.49;0; -500.56	19.01;0.07; (19-19.47)	4.34;1.56; (2.2-8.59)	12	D(Edge + TreeCov + Grass)	8	19.86;0;-430.82	16;0.02; (16-16.11)	8.13;7.15; (1.84-35.86)
13	D(Edge1 + Prey)	6	8.93;0 ;-502.39	19.01;0.08; (19-19.54)	5.57;1.52; (3.29-9.43)	13	D(Edge1 + Prey)	7	11.64;0;-430.99	16;0.02; (16-16.12)	5.5;2.81; (2.13-14.15)
14	D(Global)	8	18.51;0; -500.27	19.01;0.07; (19-19.47)	4.48;1.67; (2.21-9.08)	14	D(Global)	9	31.02;0;-430.69	16;0.02; (16-16.11)	8.74;7.95; (1.91-40.01)

No.	*Model*	*npar*	*Δ AIC; AICc weight;Log likelihood*	*$\widehat{N}$; se; lcl-ucl*	*$\widehat{D}$; se; lcl-ucl*

			PILI_2013		
15	D(1)	4	**0;0.35;** **-301.09**	25.3;1.74; (23.62- 31.57)	3.28;0.71; (2.16- 4.98)
4	D(Prey)	5	**0.49;0.27;** **-299.48**	25.16;1.68; (23.56- 31.3)	2.12;0.54; (1.3-3.46)
2	D(TreeCov)	5	2.9;0.08; -300.68	25.23;1.72; (23.59- 31.5)	2.94;0.87; (1.66-5.2)
1	D(Grass)	5	3.5;0.06; -300.98	25.3;1.73; (23.62- 31.56)	2.5;9.91; (0.09- 67.03)
6	D(Prey + TreeCov)	6	3.38;0.06; -298.82	25.07;1.65; (23.52- 31.19)	2.39;0.8; (1.26- 4.54)
8	D(Edge)	5	3.66;0.06; -301.06	25.32;1.74; (23.62- 31.61)	3.31;0.73; (2.16- 5.08)
5	D(Prey + Grass)	6	4.4;0.04; -299.33	25.14;1.67; (23.56- 31.27)	2.9;0.73; (1.78- 4.72)
13	D(Edge1	6	4.67;0.03;	25.14;1.67; (23.55-	2.78;0.67; (1.74-

	+ Prey)		-299.46	31.27)	4.44)
3	D(TreeCov + Grass)	6	6.02;0.02; -300.13	25.15;1.69; (23.55-31.35)	0.44;27.4; (0-123.22)
7	D(Prey+ TreeCov + Grass)	7	7.34;0.01; -298.38	25.01;1.62; (23.5-31.07)	2.49;0.87; (1.28-4.85)
9	D(Grass + Edge)	6	7.5;0.01; -300.88	25.32;1.74; (23.62-31.59)	3.44;0.89; (2.09-5.66)
10	D(Edge + TreeCov)	6	7.1;0.01;-300.67	25.23;1.72; (23.59-31.51)	2.95;0.96; (1.58-5.49)
11	D(Edge +* Grass)	7	12.16;0;-300.79	25.23;1.71; (23.59-31.46)	3.37;0.89; (2.03-5.61)
12	D(Edge + TreeCov + Grass)	7	10.69;0;-300.06	25.23;1.71; (23.59-31.46)	3.07;1.16; (1.5-6.27)
14	D(Global)	8	12.88;0;-298.38	24.99;1.62; (23.49-31.04)	2.34;1.02; (1.03-5.32)

No.	*Model*	*Np*	*Δ AIC; AICc weight;Log likelihood*	*N (estimate; se; lcl-ucl)*	*D (estimate; se; lcl-ucl)*
			PFC_2013		
15	D(1)	6	**0;0.23; -924.61**	50.38;2.49; (47.27-57.75)	3.4;0.51;(2.54-4.56)
1	D(Grass)	7	**1.12;0.13; -923.76**	49.97;2.38; (47.04-57.12)	1.79;1.16; (0.56-5.7)
8	D(Edge)	7	**1.33;0.12; -923.87**	51.2;2.78;(47.68-59.35)	3.14;0.57; (2.2-4.48)
4	D(Prey)	*7*	**1.5;0.11; -923.95**	50.5;2.53;(47.33-57.99)	2.9;0.55;(2-4.2)
9	D(Grass + Edge)	8	**1.66;0.1; -922.55**	50.92;2.7;(47.53-58.86)	3.36;0.63; (2.33-4.84)
2	D(Tree Cov)	7	2.77;0.06; -924.58	50.64;2.81; (47.24-59.19)	3.39;0.51; (2.53-4.56)

5	D(Prey + Grass)	8	2.82;0.06; -923.13	49.96;2.39; (47.02-57.17)	3.48;0.57; (2.54-4.77)
13	D(Edge 1 + Prey)	8	3.57;0.04; -923.5	51.12;2.77; (47.63-59.25)	3.07;0.56; (2.16-4.37)
3	D(Tree Cov + Grass)	8	4.1;0.03; -923.76	49.94;2.66; (46.84-58.28)	1.78;1.19; (0.54-5.87)
6	D(Prey + TreeCov)	8	4.46;0.03; -923.94	50.36;2.73; (47.09-58.72)	3.24;0.51; (2.39-4.4)
10	D(Edge + TreeCov)	8	4.3;0.03; -923.86	51.26;3.01; (47.56-60.32)	3.14;0.57; (2.2-4.47)
11	D(Edge +* Grass)	9	4.62;0.02; -922.45	51.07;2.76; (47.59-59.19)	3.29;0.64; (2.25-4.81)
12	D(Edge +	9	4.72;0.02;	51.07;2.76; (47.59-	3.36;0.64; (2.32-

	TreeCov + Grass)		-922.5	59.19)	4.86)
7	D(Prey + TreeCov + Grass)	9	5.84;0.01; -923.06	49.55;2.55; (46.64-57.66)	3.48;0.57; (2.54-4.78)
14	D(Global)	10	9.27;0; -923.12	51.63;3.18; (47.71-61.18)	3.36;0.62; (2.35-4.81)

Table A2.6: Median values of covariates within the region of integration for each of the study sites. These values were used to estimate a single density estimate from inhomogeneous models.

	Distance to habitat edge (median)	Distance to large grassland (median)	% Tree cover (median)	Prey density (median)
DNP	1.29	2.24	29.00	5.03
KGHAT	0.70	1.57	26.00	5.02
KPUR	1.06	2.01	34.50	10.75
PILI	1.21	1.01	33.00	10.73
PILICO MPLX	1.16	1.33	34.00	10.26

Table A2.7. Site and year specific estimates of coefficients and associated standard errors (in parentheses) for all models with Σw >=0.95. Results are for all 8 data sets from 2012 and 2013. "Significant" coefficients are in bold text. Covariate legend: Grass - distance to large grasslands; TreeCov = % tree canopy cover; Edge = distance to edge of primary habitat area; Prey- prey density for 6 ungulate species.

Site and year	new mod #	Model	AICc weight	Grass	TreeCov	Prey	Edge	Edge*Grass
			DNP 2012					
DNP '12	15	D(.)	0.4042					
DNP '12	2	D(TreeCov)	0.2469		**-0.08 (0.04)**			
DNP '12	4	D(Prey)	0.246			**0.05 (0.02)**		
DNP '12	1	D(Grass)	0.0483	-0.5 (0.45)				
			DNP 2013					
DNP '13	4	D(Prey)	0.8526			**0.09 (0.01)**		
DNP '13	6	D(Prey + TreeCov)	0.0681		-0.07 (0.04)	**0.06 (0.02)**		
DNP '13	5	D(Prey + Grass)	0.0312	0.2 (0.12)		**0.1 (0.02)**		
			Kghat 2012					
Kghat '12	1	D(Grass)	0.4753	**-0.33 (0.17)**				
Kghat '12	3	D(TreeCov + Grass)	0.1736	**-0.57 (0.25)**	0.05 (0.03)			
Kghat '12	15	D(.)	0.1305					
Kghat '12	5	D(Prey + Grass)	0.0874	**-0.39 (0.18)**		-0.03 (0.03)		
Kghat '12	9	D(Grass + Edge	0.0484	-0.32 (0.17)			0.1 (0.37)	
Kghat '12	8	D(Edge)	0.0233				0.28 (0.39)	

Kghat ‘12	2	D(TreeCov)	0.0207		-0.01 (0.03)		
			Kghat 2013				
Kghat ‘13	15	D(.)	0.4905				
Kghat ‘13	8	D(Edge)	0.1492				-0.76 (0.57)
Kghat ‘13	4	D(Prey)	0.1118			0.03 (0.02)	
Kghat ‘13	1	D(Grass)	0.0986	-0.05 (0.05)			
Kghat ‘13	9	D(Grass + Edge)	0.079	-0.06 (0.05)			-0.86 (0.58)
			Kpur 2012				
Kpur ‘12	15	D(.)	0.3843				
Kpur ‘12	2	D(TreeCov)	0.3601		**-0.05 (0.02)**		
Kpur ‘12	4	D(Prey)	0.054			0.01 (0.01)	
Kpur ‘12	8	D(Edge)	0.052				
Kpur ‘12	1	D(Grass)	0.0466	-0.05 (0.13)			
Kpur ‘12	6	D(Prey + TreeCov)	0.035		**-0.06 (0.03)**	-0.02 (0.04)	
			Kpur 2013				
Kpur ‘13	21	D(.)	0.7634				
Kpur ‘13	2	D(TreeCov)	0.0662		-0.02 (0.02)		
Kpur ‘13	8	D(Edge)	0.0635				-0.19 (0.31)
Kpur ‘13	1	D(Grass)	0.0573	-0.06 (0.17)			
			PFC 2013				
PFC ‘13	15	D(.)	0.2344				
PFC ‘13	1	D(Grass)	0.1336	-0.08			

				(0.07)				
PFC ‘13		8	D(Edge)	0.1206			-0.25 (0.22)	
PFC ‘13		4	D(Prey)	***0.1106***		0.01 (0.01)		
PFC ‘13		9	D(Grass + Edge)	0.1021	-0.1 (0.07)		-0.32 (0.23)	
PFC ‘13		2	D(TreeCov)	0.0588		0 (0.02)		
PFC ‘13		5	D(Prey + Grass)	0.0572	-0.08 (0.07)		0.01 (0.01)	
PFC ‘13		13	D(Edge1 + Prey)	0.0394			0.01 (0.01)	-0.2 (0.23)
PFC ‘13		3	D(TreeCov + Grass)	0.0302	-0.08 (0.07)	0 (0.02)		
PFC ‘13		10	D(Edge + TreeCov)	0.0273		0 (0.02)	-0.25 (0.23)	
PFC ‘13		6	D(Prey + TreeCov)	0.0253		0 (0.02)	0.01 (0.01)	
PFC ‘13		11	D(Edge1 + Prey)	0.0233	-0.06 (0.11)		-0.27 (0.25)	-0.05 (0.12)
				PILI ‘13				
PILI ‘13	15		D(.)	0.3484				
PILI ‘13	4		D(Prey)	0.2723			**0.03 (0.01)**	
PILI ‘13	2		D(TreeCov)	0.0819		0.03 (0.03)		
PILI ‘13	6		D(Prey + TreeCov)	0.0642		0.03 (0.03)	**0.04 (0.01)**	
PILI ‘13	8		D(Edge)	0.0605				-0.06 (0.31)
PILI ‘13	1		D(Grass)	0.056	-0.03 (0.18)			
PILI ‘13	5		D(Prey + Grass)	0.0337	-0.09 (0.20)		**0.03 (0.06)**	
PILI ‘13	13		D(Edge1 + Prey)	0.0385			**0.03 (0.01)**	0.06 (0.33)

Appendix 2.4. Estimating abundance and p* (cumulative detection probability over trapping period) from 'conventional' closed CR analysis in program MARK.

In order to compute the cumulative capture probability where *p** across the sampling period for each site, we estimated capture probabilities and abundance using conventional closed population models in program MARK (White and Burnham 1999). *p** was computed as $(1\text{-}p)^n$, where *p* is the per occasion capture probability, and *n* is the number of occasions -- and values of *p*(.)* indicate that all individuals in the sampled population are likely to have been captured (Gerber et al. 2014). Because the capture history matrix in conventional capture recapture modeling does not explicitly accommodate incomplete trap layout associated with block designs, we 'folded' data from multiple camera trap blocks into a single trapping block (see Karanth et al. 2002,"design 4". To explain variation in the capture process, we built models to explore potential sources of heterogeneity in detection probability arising from behavior, individual heterogeneity and a combination of these two factors (models M_b, M_h and M_{bh} *respectively*), in addition to the 'dot' model (M_0).

Table A2.8. Estimates of abundance and p* (cumulative detection probability over trapping period) from 'conventional' closed CR analysis in program MARK.

Site (year)	M_t + 1	% of individuals with no recaptures	$\widehat{N}$ (SE), CI	p, SE (model M_0),	p^*	Model selected and Model weight	Trap success (No. captures/100 trap nights)
DNP '12	14	12	14 (0.73) 14 - 18	0.26 (0.02)	1.0 ; 0.94	M_h (0.68)	5
DNP '13	14	13	14 (1.48) 14- 22	0.40 (0.03)	1.0 ; 0.99	M_{bh} (0.72)	5.6
Kishanpur '12	19	16	19 (0.58) 19 - 23	0.20 (0.01)	1.0 ; 0.97	M_h (1)	9.7
Kishanpur '13	16	15	16 (0.35) 16 - 18	0.22 (0.01)	1.0 ; 0.99	M_h (1)	9.6
Katerniaghat '12	18	15	18(0.55) 18 - 21	0.12 (0.01)	0.98	M_o (0.64)	4
Katerniaghat '13	17	16	18 (1.35) 17 - 24	0.26 (0.02)	1.0 ; 0.90	M_h (1)	6.9
Pilibhit '13	23	17	23 (0.93) 23 - 28	0.13 (0.03)	0.96	M_t (0.65)	3.3
Pilibhit Complex '13	45	18	46.22 (1.21) 45-51	0.26 (0.01)	1.0 ; 0.97	M_h(0.59)	5.9

p^* reported for model with greatest AICc support. Where the M_h model was best supported, P* has been reported separately for the two mixture groups for which detection was estimated. [++] DNP: Dudhwa NP, Kghat: Katerniaghat WLS, Kpur: Kishanpur WLS, PRF: Pilibhit Reserve Forest, PFC: Pilibhit Forest Complex.

Appendix 2.5. Assessing the effect of reducing trap area on population and detection parameter estimates (subset analysis).

Accounting for Inter-Year Variation in Survey Effort

Areas sampled with camera traps varied across years, especially in Katerniaghat Wildlife Sanctuary. Such variation in sampling area/ effort is common in multi-year camera trap monitoring programs. Sampling effort can vary from year to year, typically because of variable manpower and camera availability. Such differences in sampling can however complicate inference about population trends as demographic changes may be confounded with sampling variation. To address how variation in trap effort (area sampled with camera traps) influenced estimates of *N* and *D*, in our study, we subsampled data from 2013 to only include a fraction of camera trap locations (Fig 2.1). We predicted that estimates of density, abundance and detection parameters would be biased when the extent of the trapping grid was small relative to the overall habitat area, especially if there was pronounced spatial heterogeneity in tiger densities. We expected that the magnitude and direction of difference (+ or -) would vary depending on whether the subsampled area (subset) encompassed many or few tiger activity centers.

We limited our subset analysis to three sites: Dudhwa National Park, Katerniaghat Wildlife Sanctuary and the Pilibhit Forest Complex (Fig. 2.1, Table 2.5). The subsampled camera trap locations were drawn from regions of the Dudhwa National Park and Katerniaghat Wildlife Sanctuary that covered 32%, and 59% of the overall 2013 trapping area in these two PAs. The subset sampling frames were similar in size to areas sampled with camera traps in years prior to 2013 when overall sampling effort was lower (Table 5). For Katerniagthat WLS, we subsetted our 2013 data to match areas sampled by us in 2012. For Dudhwa National Park and the Pilibhit

Forest Complex, we subsetted data to match camera-trap coverage of previous surveys (Jhala et al., 2011). We created two separate subsampled data sets for the Pilibhit Forest Complex. In one, we retained all camera traps located within the 200 km^2 Kishanpur Wildlife Sanctuary, the only PA within PFC. In the second subsampled scenario, we only included camera traps within the boundaries of the 700 km^2 Pilibhit Forest Division, the CTL's single largest MUF. These sampling scenarios resulted in 74%, and 50% reductions in the area sampled in PFC (Fig. 2.1, Table A2.9).

To ensure that estimates of D and σ from the 'subset' and 'complete' analyses were comparable, we retained identical integration regions (area over which the tiger super-population in each site was assumed to be distributed) for the two analyses (Fig 1). This ensured that the sampling frame and target populations were constant across all analyses. Similarly, to ensure comparable estimate of tiger abundances, we used the administrative boundaries of the CTLs and PA's and MUF's used to estimate N for the complete analyses. To fit SECR models to each of the four subsets, we followed the previously described two-step procedure where we first assessed the best-supported parameterization for detection and then built 15models to test hypotheses about spatial variation in tiger density, with regard to the four key covariates (*Prey, TreeCov, Grass and Edge*) (Fig A1). We compared estimates for key parameters between homogenous models, at the median value of the four covariates and computed the magnitude and direction (- or +) of differences.

Influence of Varying Survey Effort on Density Estimates

For the subset analyses, the first modeling step entailed using a global parameterization on density to explore sources of heterogeneity in the detection process (six alternate models). The

mixture model structure *[g0(.), σ(sex)]* was supported in two subset analyses. The parameterization *[(g0(.) σ(.)] and [a0(.), σ(sex)]* were the best supported detection parameterizations in the two other subset model sets Table A2.9). There was agreement in the best supported detection parameterization between the subset and complete analyses only in Dudhwa NP (2013).

Subset analysis indicated that when the area sampled with camera traps was small relative to the distribution of tigers, estimates of density, abundance and σ were likely to be both biased and imprecise. For Dudhwa NP in 2013, a 59% reduction extent of the trap array resulted in captures of 10 unique adult tigers, four fewer than the 'complete' analysis. Supported models *D*(*TreeCov)* yielded estimates that were lower than corresponding estimates from the complete models (Fig. A2.5). Estimates of σ from the subset analysis were 5% and 13% smaller for females and male tigers respectively (Table 2.5). For the Katerniaghat subset analysis, (trap area reduction of 32 %) yielded captures of 15 of the 16 tigers in the complete data set. Density estimates for supported subset models were 5-10% lower that estimates from the complete models, whereas estimates from the *Prey*, *Edge* and '*dot*' models were 5-11% higherModel averaged estimates of σ for the complete and subset models were not directly comparable for Katerniaghat because the detection parameters were different for the complete and subset analyses (for example, sex effects on σ may have been supported in the complete analysis yielding two separate estimates of σ, while σ(.) may have been better supported for the subset models) (Table A2.8, Appendix S2, Table A2.1, Appendix 2.5, Table A2.8). Of the 45 adult tigers captured in PFC, 16 were present within Kishanpur subset and 23 individuals in the Pilibhit subset. In the Kishanpur subset (74% reduction in trap area of PFC), the best supported model D(.) (w=0.78) provided estimates that were 31.8% higher than the corresponding model from the complete analysis. By contrast, the

best supported models for the Pilibhit subset, *D(.)* and *D(Prey)* yielded estimates that were -3% and -35% lower respectively, than the corresponding models in the complete analysis. Model averaged σ estimates from the Kishanpur subset analyses were -39% and -42% smaller for males and females respectively, than for the complete analyses (Fig A2.1). Subset model estimates of σ were similar to complete model estimates for the Pilibhit subset (Appendix 2.5, Table A2.10). Across all the subset analyses, confidence interval coverage for supported models were overlapping, but wider than corresponding CI's from the complete model set (Appendix 2.3).

Table A2.9. Summary of camera trapping 'effort' and tiger capture for the subset analyses. The Katerniaghat subset reflects the area we sampled in 2012. Other subsets reflect survey effort of previous studies (Jhala et al., 2010).

Site	Number of camera locations	average spacing (km)	trap nights	% decrease in trap array footprint relative to complete data	No. of detections	No. of individuals captured	How much larger/smaller are estimates of detection parameters from complete analysis, relative to subset				
							g0-F	g0-M	sigma-F	sigma-M	pmix-M
DNP_{subset}	94	1.1	2306	59	166	10	20	20	-5.11	-13.27	-20.51
$Katerniaghat\_{subset}$	84	1.3	2605	32	175	15	0	0			29.79
$PiliComplex_{subsetPilibhit}$	171	2	2814	74	94	23			-39.16	-42.35	5.13
$Pilicomplex_{subsetKishanpur}$	67	1.5	2655	50	256	15			0.007	0.008	0

Table A2.10. Summary of model selection results to assess optimal detection parameterization for four subset analyses(Dudhwa National Park, Katerniaghat Wildlife Sanctuary and two alternate subset scenarios for the Pilibhit Forest Complex) . In all models, a 'global' model structure (D(Grass + Prey + EdgeDist + TreeCov) was used to model variation in density. ΔAICc and AICc weights (in parentheses) are reported for 6 alternate parameterizations of detection parameters (columns). Models that garnered high AICc support are in bold text.

Site/ model	g_0(sex) sigma(sex) pmix(sex)	g_0 (.) sigma(sex) pmix(sex)	g_0 (sex) sigma(.) pmix(sex)	g_0 (.) sigma(.) pmix(sex)	a_0(.) sigma(.) pmix(sex)	a_0(.) sigma(sex) pmix(sex)
No. of parameters	10	9	9	8	8	9
DNP subset	- 353.74;1.19(0.31)	- **354.33;0(0.55)**	- 364.93;19.26(0)	- 366.04;21.12(0)	- 366.04;22.85(0)	- 357.91;2.74(0.14)
Kghat subset	- 364.69;20.71(0)	- 366.7;3.73(0.07)	- 371.42;13.15(0)	- **371.84;0(0.42)**	- 371.84;0(0.42)	- 366.38;3.08(0.09)
PFC Kishanpur subset	- 429.9;14.42(0)	- 437.23;13.09(0)	- 441.61;21.84(0)	- 442.67;12.54(0)	- 448.55;24.3(0)	- **430.69;0(1)**
PFC Pilibhit subset	- 293.85;4.97(0.07)	- **294.61;0(0.89)**	- 301.03;12.84(0)	- 302.17;9.56(0.01)	- 302.17;9.56(0.01)	- 298.38;7.53(0.02)

[++] DNP: Dudhwa NP, Kghat: Katerniaghat WLS, Kpur: Kishanpur WLS, PRF: Pilibhit Reserve Forest, PFC: Pilibhit Forest Complex.

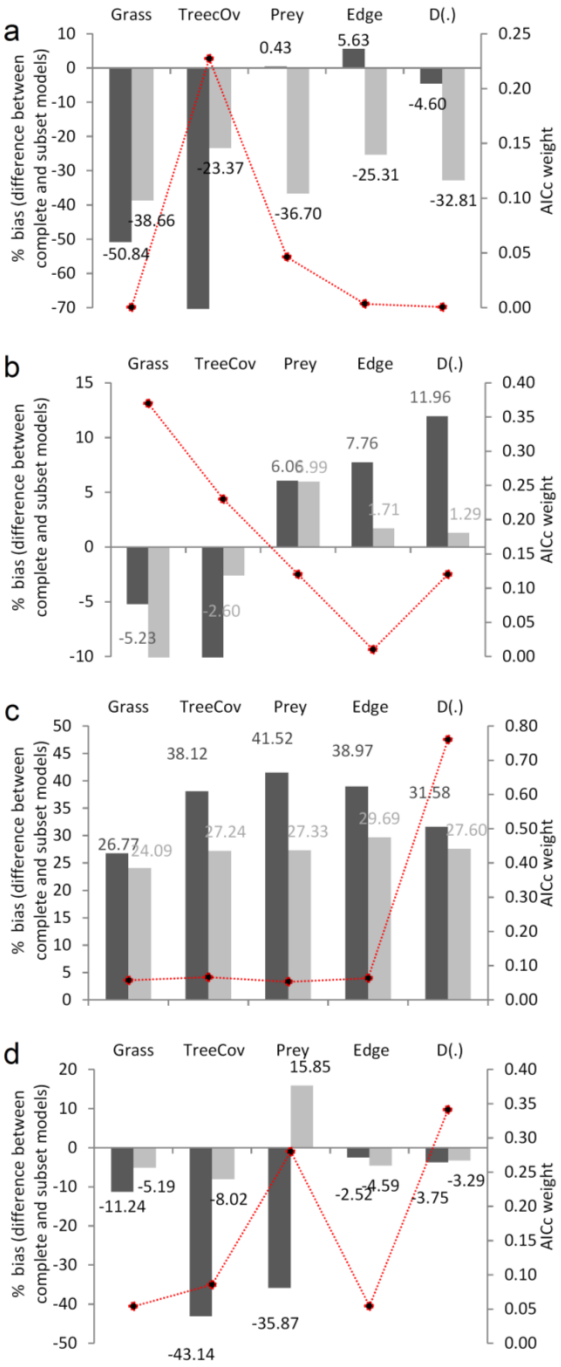


Figure A2.1Percent difference between estimates of tiger density for subset models relative to models from the complete analyses. a: Dudhwa National Park; b: Katerniaghat Wildlife Sanctuary; c. Pilibhit Complex (Kishanpur subset); d. Pilibhit Complex (Pilibhit subset).

Table A2.11. Table of model selection results and estimates of density and abundance for the subset analyses for DNP, Katerniaghat, and Pilibhit Complex (2 scenarios) from 2013 data. Covariate legend: Grass - distance to large grasslands; TreeCov = % tree canopy cover; Edge = distance to edge of primary habitat area; Prey- prey density for 6 ungulate species.

No.		npar	Δ AIC; AICc weight;Log likelihood	$\widehat{N}$; se; lcl-ucl	$\widehat{D}$; se; lcl-ucl
			DNP subset		
2	D(TreeCov)	6	0;0.23;-355.43	12.24;1.86;(10.54-19.25)	0.23;0.47;(0.02-2.85)
3	D(TreeCov + Grass)	7	0.17;0.21;-354.42	10.68;1.05;(10.08-15.94)	0;143.91;(0-9.56)
6	D(Prey + TreeCov)	7	0.35;0.19;-354.51	11.32;1.49;(10.22-17.78)	0.2;0.57;(0.01-3.71)
10	D(Edge + TreeCov)	7	2.16;0.08;-355.42	12.23;1.86;(10.54-19.27)	0.2;0.81;(0.01-5.49)
12	D(Edge + TreeCov + Grass)	8	2.23;0.07;-354.35	10.77;1.01;(10.11-15.49)	0.02;0.63;(0-3.25)
7	D(Prey+ TreeCov + Grass)	8	2.32;0.07;-354.39	10.78;1.31;(10.08-17.55)	0.05;16.96;(0-40.01)
4	D(Prey)	6	3.19;0.05;-357.02	10.36;0.64;(10.04-13.71)	0.58;0.36;(0.19-1.76)
13	D(Edge1 + Prey)	7	3.27;0.04;-355.97	11.34;1.59;(10.21-18.39)	1.28;0.6;(0.53-3.06)
5	D(Prey + Grass)	7	4.21;0.03;-356.44	10.88;1.21;(10.12-16.65)	1.08;0.53;(0.43-2.7)
14	D(Global)	9	4.43;0.02;-354.33	10.69;1.19;(10.07-16.9)	0.02;28.28;(0-38.62)

8	D(Edge)	6	8.39;0;-359.62	11.92;1.59;(10.47-17.94)	1.67;0.72;(0.74-3.77)
9	D(Grass + Edge)	7	9.63;0;-359.15	11.09;1.29;(10.18-16.82)	1.55;0.71;(0.66-3.64)
11	D(Edge +* Grass)	8	11.39;0;-358.93	11.34;1.59;(10.21-18.39)	0.92;4.37;(0.03-29.96)
15	D(1)	5	12.32;0;-362.66	10.96;1.04;(10.17-15.41)	1.8;0.59;(0.96-3.38)
1	D(Grass)	6	13.74;0;-362.3	10.47;0.8;(10.05-14.59)	0.08;1869.64;(0-539.81)

No.			Δ AIC; AICc weight;Log likelihood Kghat $_{subset}$	$\widehat{N}$; se; lcl-ucl	$\widehat{D}$; se; lcl-ucl
1	D(Grass)	5	0;0.37;-372.74	15.02;0.13;(15-15.86)	0.08;0.76;(0-5.19)
2	D(TreeCov)	5	0.96;0.23;-373.22	16.67;1.45;(15.38-22.27)	0.84;1.39;(0.09-7.95)
4	D(Prey)	5	2.25;0.12;-373.87	18.23;2;(16.06-24.87)	2.13;0.79;(1.06-4.3)
15	D(1)	4	2.31;0.12;-376.23	17.34;1.65;(15.67-23.14)	3.26;0.86;(1.96-5.43)
5	D(Prey + Grass)	6	4.12;0.05;-371.88	15.02;0.15;(15-16.07)	3.25;1;(1.81-5.86)
3	D(TreeCov + Grass)	6	4.73;0.04;-372.19	15.04;0.24;(15-16.64)	0.19;1.16;(0-7.99)
9	D(Grass + Edge)	6	5.77;0.02;-372.71	15.02;0.13;(15-15.87)	3.28;1.15;(1.69-6.38)
6	D(Prey + TreeCov)	6	6.06;0.02;-372.86	17.07;1.72;(15.5-23.56)	1.11;2.02;(0.1-11.87)
10	D(Edge + TreeCov)	6	6.79;0.01;-373.22	16.67;1.46;(15.38-22.3)	0.84;1.5;(0.08-8.8)
8	D(Edge)	5	6.9;0.01;-376.19	17.43;1.72;(15.7-23.47)	3.1;1.07;(1.6-5.98)

13	D(Edge1 + Prey)	6	7.93;0.01;-373.79	15.75;3.71;(15.02-40.5)	3.21;1.05;(1.72-6)
11	D(Edge +* Grass)	7	10.09;0;-371.12	15.75;3.71;(15.02-40.5)	1.06;3.96;(0.04-26.61)
7	D(Prey+ TreeCov + Grass)	7	11.53;0;-371.84	15.03;0.2;(15-16.37)	2.67;2.62;(0.53-13.36)
12	D(Edge + TreeCov + Grass)	7	12.19;0;-372.17	18.05;1.99;(15.95-24.8)	1.8;2.1;(0.29-11.06)
14	D(Global)	8	21.53;0;-371.84	15.03;0.2;(15-16.38)	2.71;2.75;(0.52-14.08)
No.			Δ AIC; AICc weight;Log likelihood PFC $_{\text{Kishanpur Subset}}$	$\widehat{N}$; se; lcl-ucl	$\widehat{D}$; se; lcl-ucl
15	D(1)	4	**0;0.32;-430.38**	69.58;15.33;(46.92-108.84)	4.97;1.27;(3.04-8.12)
2	D(TreeCov)	5	**1.15;0.18;-430.95**	69.59;15.36;(46.9-108.94)	4.4;1.47;(2.33-8.31)
8	D(Edge)	5	**1.24;0.17;-431**	72.83;17.02;(47.99-116.94)	5.97;2.39;(2.81-12.69)
1	D(Grass)	5	**1.44;0.15;-431.1**	65.82;15.98;(42.98-108.01)	2.49;13.32;(0.07-91.83)
4	D(Prey)	5	**1.59;0.14;-431.17**	69.49;15.31;(46.86-108.7)	4.93;1.34;(2.92-8.32)
10	D(Edge + TreeCov)	6	7.69;0.01;-430.89	71.64;16.86;(47.13-115.45)	5.11;2.88;(1.83-14.29)

6	D(Prey + TreeCov)	6	7.71;0.01;-430.9	69.84;15.51;(46.96-109.62)	4.38;1.49;(2.29-8.39)
9	D(Grass + Edge)	6	7.71;0.01;-430.9	68.56;17.23;(44.1-114.32)	2.71;16.05;(0.07-110.86)
3	D(TreeCov + Grass)	6	7.73;0.01;-430.91	66.62;16.65;(43.01-110.88)	2.64;13.16;(0.08-90.53)
13	D(Edge1 + Prey)	6	7.91;0.01;-431	70.14;20.16;(42.71-125.72)	6.13;2.79;(2.62-14.34)
5	D(Prey + Grass)	6	8.11;0.01;-431.1	65.85;16.06;(42.93-108.3)	2.5;13.66;(0.07-94.26)
12	D(Edge + TreeCov + Grass)	7	16.12;0;-430.82	74.04;17.31;(48.76-118.84)	2.72;14.8;(0.07-102.06)
7	D(Prey+ TreeCov + Grass)	7	16.16;0;-430.84	66.67;16.32;(43.38-109.8)	2.41;12.31;(0.07-84.76)
11	D(Edge +* Grass)	7	16.19;0;-430.85	70.14;20.16;(42.71-125.72)	4.19;52.27;(0.05-343.43)
14	D(Global)	8	27.29;0;-430.69	68.73;16.8;(44.67-112.98)	2.27;13.41;(0.06-92.62)

No.		npar	Δ AIC; AICc weight;Log likelihood PFC Pilibhit Subset	$\widehat{N}$; se; lcl-ucl	$\widehat{D}$; se; lcl-ucl
15	D(1)	6	0;0.32;-430.38	69.58;15.33;(46.92-	4.97;1.27;(3.04-8.12)

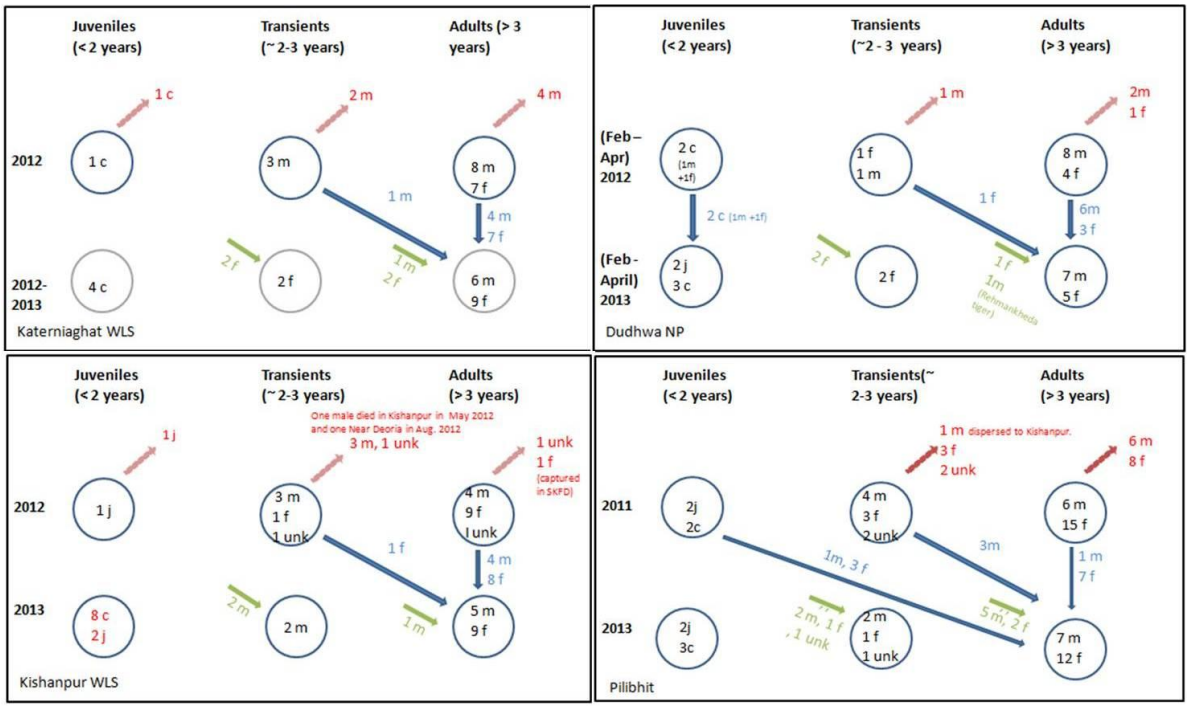
				108.84)	
2	D(TreeCov)	6	1.15;0.18;-430.95	69.59;15.36;(46.9-108.94)	4.79;1.29;(2.85-8.05)
8	D(Edge)	6	1.24;0.17;-431	72.83;17.02;(47.99-116.94)	4.86;1.32;(2.89-8.18)
1	D(Grass)	6	1.44;0.15;-431.1	65.82;15.98;(42.98-108.01)	2.86;8.06;(0.16-52.07)
4	D(Prey)	6	1.59;0.14;-431.17	69.49;15.31;(46.86-108.7)	4.87;1.65;(2.56-9.29)
10	D(Edge + TreeCov)	7	7.69;0.01;-430.89	71.64;16.86;(47.13-115.45)	4.79;1.3;(2.84-8.07)
6	D(Prey + TreeCov)	7	7.71;0.01;-430.9	69.84;15.51;(46.96-109.62)	4.84;1.32;(2.86-8.19)
9	D(Grass + Edge)	7	7.71;0.01;-430.9	68.56;17.23;(44.1-114.32)	5.01;1.35;(2.98-8.42)
3	D(TreeCov + Grass)	7	7.73;0.01;-430.91	66.62;16.65;(43.01-110.88)	3.18;8.58;(0.18-54.97)
13	D(Edge1 + Prey)	7	7.91;0.01;-431	70.14;20.16;(42.71-125.72)	5.02;1.35;(2.98-8.43)
5	D(Prey + Grass)	7	8.11;0.01;-431.1	65.85;16.06;(42.93-108.3)	5.06;1.34;(3.03-8.44)
12	D(Edge + TreeCov + Grass)	8	16.12;0;-430.82	74.04;17.31;(48.76-118.84)	4.91;1.35;(2.89-8.33)
7	D(Prey+ TreeCov + Grass)	8	16.16;0;-430.84	66.67;16.32;(43.38-109.8)	4.94;1.37;(2.89-8.43)

11	D(Edge +* Grass)	8	16.19;0;-430.85	70.14;20.16;(42.71-125.72)	4.84;1.49;(2.69-8.72)
14	D(Global)	9	27.29;0;-430.69	68.73;16.8;(44.67-112.98)	5.06;1.44;(2.93-8.75)

Table A2.12. Model averaged estimates of σ, g0 and p_{mix} (sex-ratio) for the 4 subset analyses from 2013 data.

Model averaged	DNP_{subset}	$Kghat_{subset}$	$PFC_{Kishanpur\ subset}$	$PFC_{Pilibhit\ subset}$
$\widehat{D}$ (se)	3.53(336.7)	5.67(3.19)	4.83(2.3)	2.79(2.96)
CI $\widehat{D}$	NA-NA	2.03-15.85	1.99-11.72	0.51-15.29
g_0 F(se)	0.05(0.006)	0.05(0.01)	0.1(0.01)	0.03(0.001)
g_0 F (CI)	NA-NA	0.04-0.06	0.08-0.13	0.02-0.03
g_0 M(se)	0.05(0.006)	0.05(0.01)	0.05(0.01)	0.03(0.001)
g_0 F (CI)	NA-NA	0.04-0.06	0.04-0.07	0.02-0.03
σ F (se)	2676(4390)	3572.49(229.6)	1648.78(92.6)	2294.67(232.41)
σ F (CI)	NA-NA	3150.07-4051.54	1477.06-1840.47	1882.47-2797.12
σ M (se)	4391(259.6)	3572.49(229.6)	2636.45(194.71)	3753.27(350.71)
σ M (CI)	NA-NA	3150.07-4051.54	2281.62-3046.47	3126.4-4505.82
pmixM(se)	0.39(0.16)	0.47(0.13)	0.39(0.12)	0.37(0.1)
Pmix (CI)	NA-NA	0.24-0.71	0.19-0.64	0.2-0.59

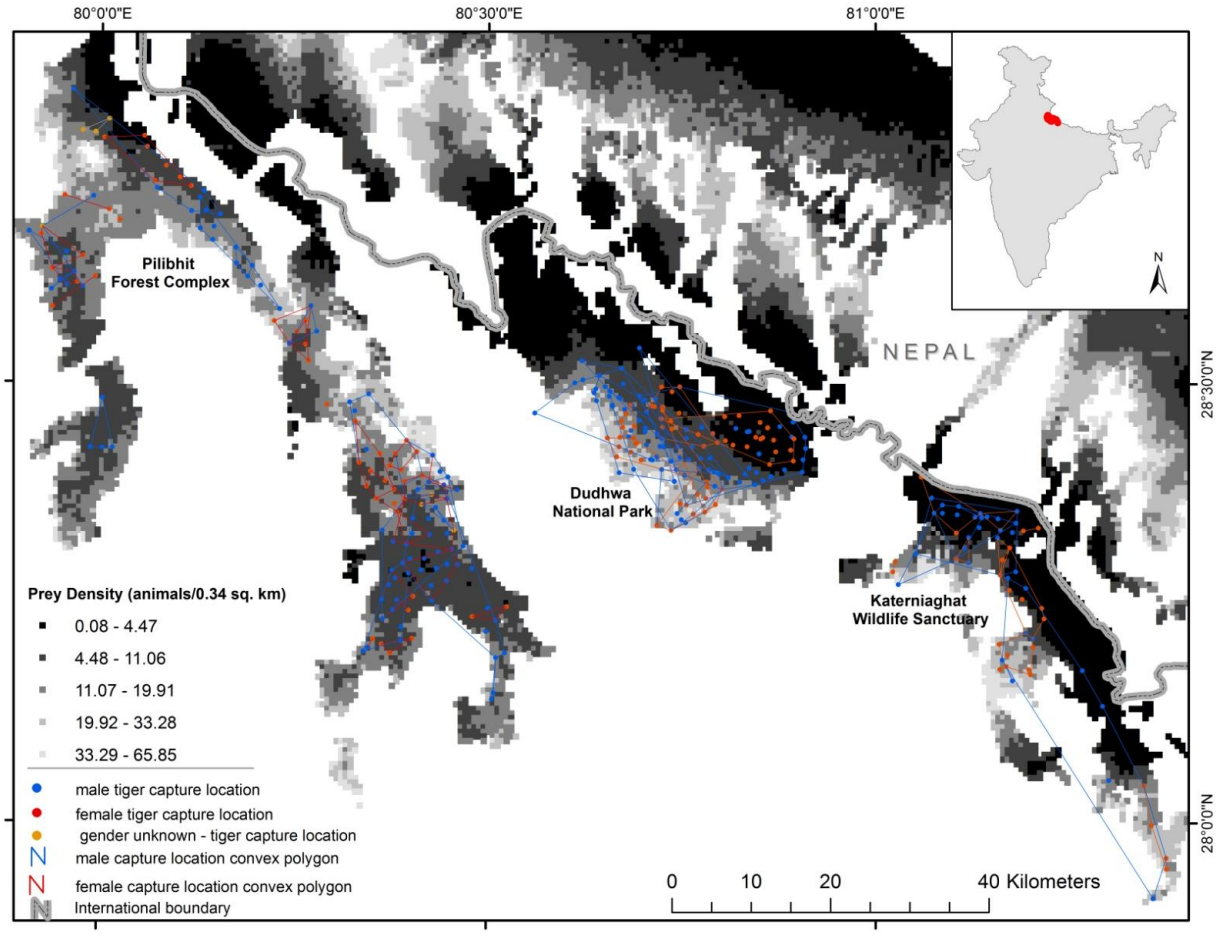
Appendix 2.6: Information on inter-annual "turn-over" of tigers over the two study years. Data from Pilibhit from 2011 are also reported. These data were not considered for density/ abundance estimation in the current study because the time span over which they were collected exceeded the stipulated 45-60 day sampling period. This figure has been reproduced from Chanchani et al., 2014.



FigA 2.2**:** Age and sex characteristics and stage transitions recorded for the four tiger-occupied areas sampled in the CTL in 2012-2013 (with the exception of Pilibhit, first sampled in 2011). The upper row in each figure represents the population composition (depicted by gender and age class) during the first sampling season (2011/2012). The lower row in each figure depicts this information for the second sampling season (ie., 2013). Each circle represents a single age class (juveniles, transients or adults). Juveniles below the age of (.) are referred to as cubs (c) , while transients refers to individuals in the 2-3 year age class. Numbers within the circles are counts of individuals in a given age class, and the notations 'm', 'f' and 'unk' index male, female and

animals of unknown sex respectively. Individuals indexed with a *j* in the first season will transition to the transient age class in the second sampling season, assuming that they survive and are detected. Cubs (*c*), detected i9n the first season, on the other hand, will stay in the same age class, and will be indexed as *j* in the second season. The blue arrows indicate the direction of stage transitions, and the numbers printed above blue lines (also in blue) are counts of animals that were known to survive the interval, and transition from one age class to the next. Red arrows and associated counts in red annotate individuals that were in the population in the first season, but were not detected in the second season (these animals either did not survive, immigrated permanently, or remained in the population but went undetected in the second season's surveys). Green arrows and associated counts index individuals that 'entered' the sampled populations in 2013. These individuals were either present in the population in the previous season (and went undetected), or emigrated into the population between the two sampling seasons.

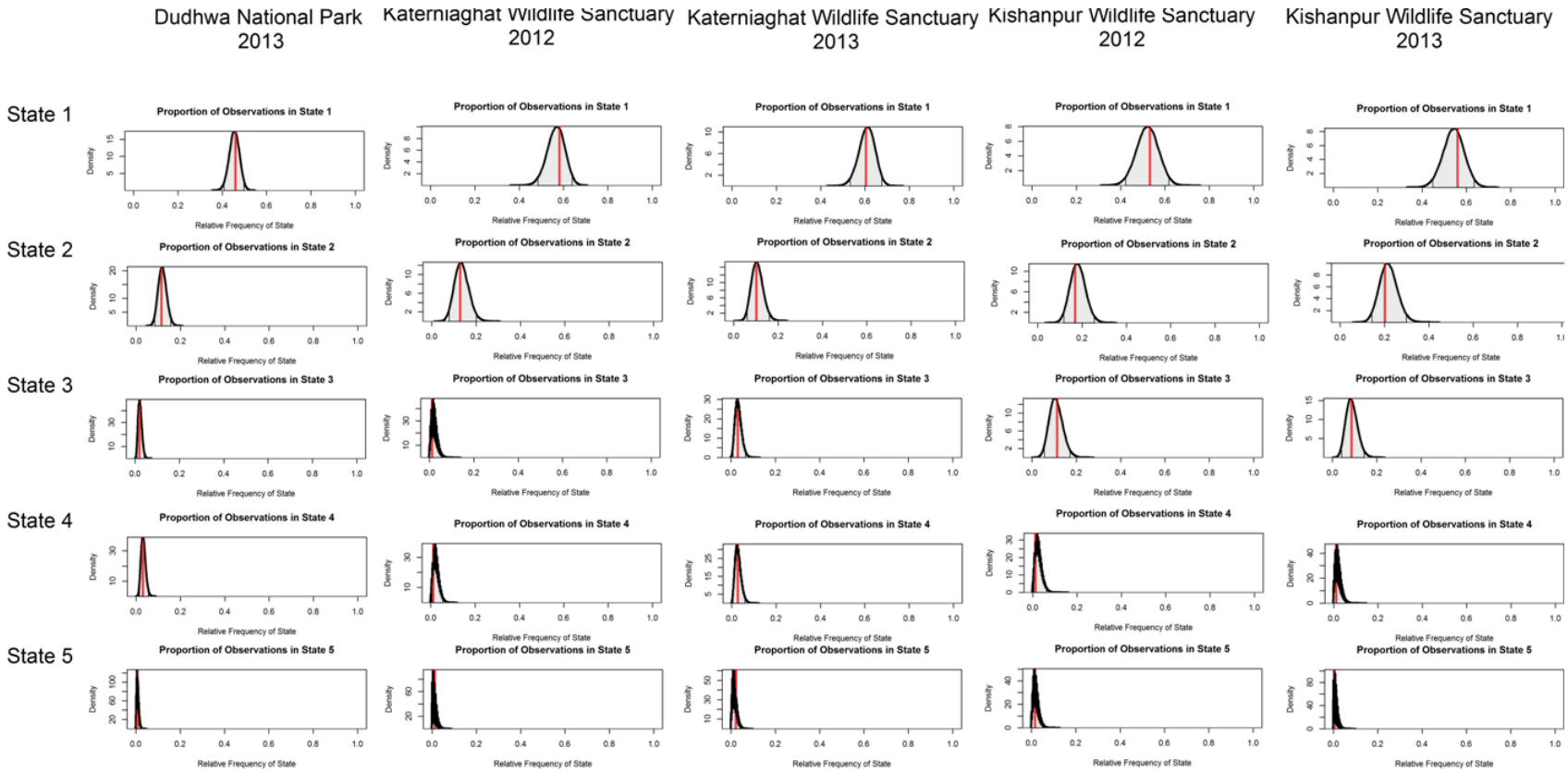
Appendix 2.7: Approximate home ranges of tigers 'photo captured' on camera traps during the 2 years sampling period relative to the density of ungulate prey species.



FigA2.3. Map depicting capture locations and /or minimum convex polyg0ns (MCPs) connecting camera stations where 92 individual tigers were captured over the 2012 and 2013 sampling seasons. Capture locations of male and female tigers, and associated MCPs have been depicted in different colors. The background map (of primary tiger habitats in the CTL) has been color coded to illustrate spatial heterogeneity in ungulate prey density (seven species combined: chital, wild pigs, nilgai, hogdeer, swamp deer, barking deer and sambar). This map is a rendition of the predicted output of the density surface model for tiger prey species developed from line

transect data (see Appendix 1). MCP's can only be generated for tigers that were captured at atleast 3 distinct trap stations over the study period 20 tigers in our study did not meet this criteria, and thus appear on this map only as 1-2 point locations with no associated

APPENDIX 3.1. Posterior predictive check plots. Grey distributions represent the of relative frequency of various values in a simulated data set (generated from the model). The red line represents the relative frequency of tiger occurrences in a given state in the original data.



APPENDIX 3.2. Model selection results for open-population (CJS) models to estimates apparent survival for tigers in DTR.

	Model	AICc	ΔAICc	AICc Weights	Model Likelihood	Parameters	Deviance
Dudhwa	Phi(.) p(.)	71.01	0.00	0.46	1	2	66.71
	Phi(.) p(sex)	72.15	1.14	0.26	0.57	3	65.54
	Phi(sex) p(.)	72.73	1.72	0.19	0.42	3	66.12
	Phi(sex) p(sex)	74.21	3.20	0.09	0.20	4	65.16
Katerniaghat	Phi(.) p(.)	80.81	0.00	0.51	1	2	76.56
	Phi(.) p(sex)	82.47	1.66	0.22	0.44	3	75.95
	Phi(sex) p(.)	83.06	2.25	0.17	0.32	3	76.55
	Phi(sex) p(sex)	84.20	3.39	0.09	0.18	4	75.33
Kishanpur	Phi(sex), p(.)	70.36	0.00	0.38	1	3	63.82
	Phi(.), p(.)	70.65	0.29	0.33	0.87	2	66.39
	Phi(sex), p(sex)	72.06	1.69	0.16	0.43	4	63.13
	Phi(.), p(sex)	72.51	2.15	0.13	0.34	3	65.96